*Proceedings of the Workshop on
Biological Control of Heliothis:
Increasing the Effectiveness
of Natural Enemies*

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IOBC HELIOTHIS WORK GROUP

New Delhi, India
11–15 November 1985

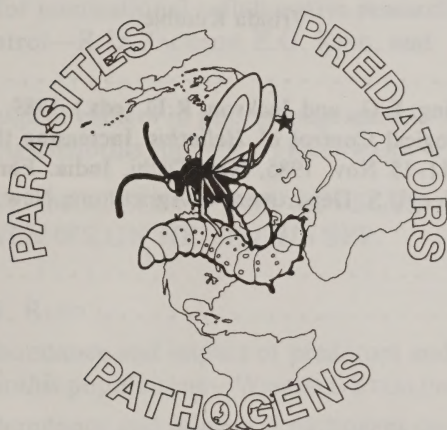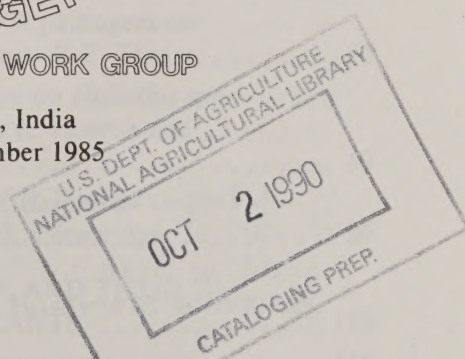# Proceedings of the
Workshop on Biological Control of Heliothis:

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Far Eastern Regional Research Office
Office of International Cooperation & Development (OICD)
U.S. Department of Agriculture
Chanakya Puri, New Delhi, India
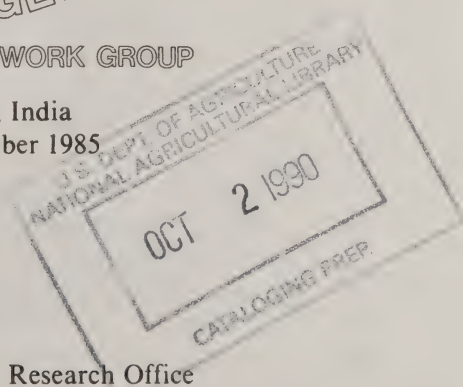1989

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Objectives of the Workshop

(a) To document the importance of natural enemies attacking *Heliothis* and

(b) To identify research needed for developing strategies to increase the effectiveness of natural enemies.

Preface

The International *Heliothis* Biological Control Work Group, an affiliate of the International Organization of Biological Control of Noxious Pests and Weeds, suggested the workshop "Biological Control of *Heliothis*: Increasing the Effectiveness of Natural Enemies" as a topic for celebration of the Silver Jubilee in Cooperative Agricultural Research between the Indian Council of Agricultural Research and the Far Eastern Regional Research Office of the Office of International Cooperation and Development, U.S. Department of Agriculture. These Proceedings fulfill the workshop general objectives, i.e., "to document the importance of natural enemies attacking *Heliothis* and identify research needed to develop strategies for increasing their effectiveness." More specifically, ideas and research approaches were stimulated and promoted, information was disseminated, pathways for obtaining funds to conduct research were identified, recommendations were developed to serve as guidelines for future research, and the proceedings were published for examination by the scientific community.

The workshop and the Proceedings were organized and described within the context of integrated pest management (IPM). IPM emphasizes movement away from reliance upon a single control procedure toward the use of all available management methods. A generally accepted component of IPM strategy is the conservation and maximum use of natural enemies. For purposes of these Proceedings biological control may be defined as the management of predators, parasites, and pathogens (natural enemies) and their products to reduce pest population densities and their effects.

The value of natural enemies in the regulation of *Heliothis* populations is described in Subtopic I of the Proceedings "Measuring and modeling the effects of natural enemies." Parasites, predators, and pathogens, which attack *Heliothis* throughout their geographic range as well as the host plants of *Heliothis*, are catalogued in a series of papers from India, Pakistan, People's Republic of China, Australia, Western Europe, and the Western Hemisphere in Subtopic II, "Distribution of *Heliothis* and their natural enemies and host plants." Attempts to import and establish new, more effective natural enemies of *Heliothis* are documented in Subtopic III, including the successful establishment of the braconid *Cotesia kazak* on *Heliothis armigera* in New Zealand. Efforts to augment biological control of *Heliothis* through propagation and release or application of natural enemies and using behavior-modifying chemicals to manage dis-

persal and prey or host finding are discussed in Subtopic IV, "Increasing the effectiveness of natural enemies." Subtopic V, "integration of biological control into crop production systems" treats other control approaches—cultural, host-plant resistance, and chemical—as components of an overall IPM and crop-management strategy that fully considers and utilizes natural enemies yet emphasizes timely and economic production of affected commodities.

R.W. Poole in Subtopic II, Chapter 3, "A general synopsis of the systematics of *Heliothis* and *Helicoverpa*" agreed with D.F. Hardwick, i.e., members of the corn earworm complex are morphologically distinct from *Heliothis* species and are not closely related phylogenetically. Nevertheless, for purposes of these Proceedings, *Heliothis* is used as the nominate genus including *Heliothis* (in the strict sense) and the less often recognized *Helicoverpa* as a subgenus. Concern was strongly expressed by participants over the potential inconvenience and confusion related to changing the genus name applied to members of the corn earworm complex. Whatever the specific or generic confines, we must seek to understand those general principles that pertain to *Heliothis* as a taxon as well as deal with the uniqueness of each species because differences important to the potential for biological control do exist.

Edgar G. King and Robert D. Jackson

Recommendations

Recommendations

Recommendations

MEASURING AND MODELING THE EFFECT OF NATURAL ENEMIES ON *HELIOTHIS* SPP. POPULATIONS

The group concluded that the ability to estimate and predict the impact of the natural enemy complex on *Heliothis* populations, and of the crop losses caused by these, are essential for well-planned biological control and other integrated pest management action on crops. The value of the yield difference resulting from the natural enemy impact should be quantified in monetary terms.

Although methodologies to estimate and model such impact for a generation of *Heliothis* on individual crops exist, they are seldom adequately utilized. In most situations, the key natural mortality factors have not been determined, and there is usually a conspicuous lack of available data, particularly concerning the predators and their value. A lack of knowledge concerning the movement of *Heliothis* moths and the natural enemies prevents us from estimating the effects of natural enemies across areas or seasons.

The group recommends that further research is necessary and should be encouraged on:

1. Movement of *Heliothis* moths and the natural enemies between host plants and areas.

2. Identification, quantification, and assessment of the impact of predators.

3. Identification of key species of predators, parasites, and pathogens, through the use of *Heliothis* life table studies.

4. Modeling, for which there is a particular need to measure search rates, life tables, and spatial distribution of the key parasites and predators, and the quantitative host/pathogen relationships as affected by the host plant and relevant abiotic factors.

DISTRIBUTION OF *HELIOTHIS* AND THEIR NATURAL ENEMIES AND HOST PLANTS

Because improved methodologies and additional material are now available, the group felt that more support should be made available for

detailed biosystematic research on the Heliothinae. The need for extensive surveys to determine the precise distribution of the Heliothinae and their natural enemies was stressed, as well as the need for developing uniform methods for collecting data and for disseminating information. It was felt that such information would facilitate international cooperation in the area of biological control. The group made the following recommendations:

1. Promote surveys of Heliothinae and natural enemies over wide geographical areas in relation to host plants.
2. Encourage more biosystematic research on the *Heliothis* complex above the species level and on the *Heliothis* complex below the species level.
3. Study natural enemy complexes in different cropping systems/agro-ecosystems and natural ecosystems. Increased effort should be made to study the role of predators.
4. Develop means to guarantee competent taxonomic services for pests and natural enemies. Support must be given to national and regional taxonomic research and service units, such as the Biosystematics Research Institute, Agriculture, Canada; Commonwealth Institute of Entomology; Biosystematics and Beneficial Insects Institute, U.S. Department of Agriculture; and international efforts such as the International Advisory Committee for Biosystematic Services in Entomology.
5. Enlist assistance of groups like the IOBC *Heliothis* Biological Control Work Group in developing protocols (at least on a regional basis) for uniform data gathering on pests and natural enemies, both for surveys and experimental studies, and to facilitate data storage and analysis.
6. Support efforts to make information on pests and natural enemies readily available to workers. Encourage communication and cooperation among database managers in the areas of biological control, biosystematics, and other areas that impinge on biological control of natural enemies.
7. Develop improved means for promoting exchange of natural enemies.

EXPLORATION, IMPORTATION, AND ESTABLISHMENT OF NEW EFFECTIVE NATURAL ENEMIES OF *HELIOTHIS*

1. Supporting agencies should recognize and provide the long-term financial support needs of biological control programs.
2. Selection of natural enemies to be utilized should be based on scientific study and should be imported from different ecological areas.
3. Restrictive regulations should be avoided to facilitate the exchange of natural enemies.

4. Binational agreements should include provisions for exchange of natural enemies.

5. Parasites to be exchanged should include, but not be limited to, the following genera: *Apanteles, Cotesia, Bracon, Campoletis, Cardiochiles, Obelonus, Copidosoma, Hyposoter, Microplitis, Telenomus, Trichogramma,* and *Trichogrammatoidea.*

INCREASING THE EFFECTIVENESS OF NATURAL ENEMIES FOR SUPPRESSION OF *HELIOTHIS* POPULATIONS

Numerous attempts have been made to enhance the effectiveness of both native and exotic natural enemies but without substantial success, largely because of insufficient knowledge on the biology and behavior of the natural enemies and their ability to sustain environmental stresses. To understand the factors responsible for this ineffectiveness and to develop approaches to enhance natural enemy effectiveness, more research is required, especially on the following aspects:

Insect Pathogens

1. Improved strains of microbial biological control agents are needed if they are to be effective in agronomic applications. However this is accomplished (through selection, genetic modification, or genetic engineering), appropriate assays need to be developed at the genetic and biochemical level for the particular characteristic which requires improvement.

2. Improvements in formulation and application technology for microbial agents are needed. Critical factors include stability in storage and transport, protective adjuvants, timing applications, and improved methods of application.

3. To conserve time and resources, it is recommended that the existing data on safety evaluation of *Heliothis* NPV be utilized for registration purposes by developing countries. Further, the possibility of collaboration between the public and private sectors should be explored for the development of formulations and application techniques for microbial pathogens.

Parasites/Predators

4. Develop a better understanding of how semiochemicals and other factors govern foraging behavior, dispersal, and other aspects of *Heliothis*-natural enemy relations and design ways to use this information to increase successes within importation, augmentation, and conservation programs.

5. Interdisciplinary teams should be formed to develop mass propagation technology for selected predators and parasites for use in augmenta-

tion programs, including the development of artificial diets, *in vitro* rearing procedures, where feasible, and use of genetically improved biotypes.

6. Conduct field trials using rigorous experimental techniques to evaluate the technical and economic feasibility of controlling *Heliothis* by augmentative releases of selected parasites and predators within cropping systems.

INTEGRATION OF BIOLOGICAL CONTROL INTO CROP PRODUCTION SYSTEMS

Changing agricultural practices in many countries have often increased the pest status of *Heliothis*. No single approach can be depended on for control of *Heliothis*. It is imperative that systems for controlling *Heliothis* include biological control as a component. Manipulation of the crop production system is probably one of the least exploited, but most effective techniques available for control. Often, there is a conflict between biological control and other insect control techniques used. Two examples are host plant resistance and particularly the use of insecticides. Obviously, there is a need for coordination in the development and implementation of changes to the basic cropping system.

1. Ecological and biochemical effects of host plants on natural enemies of *Heliothis*. The interrelationships between host plants, *Heliothis*, its natural enemies, and their hyperparasites involve poorly understood phenomena. The following represent the major areas of concern which need to be elucidated by future research:

    a. Influence of host plants, weeds, and associated flora on the interaction of *Heliothis* and its natural enemies.

    b. Host plant resistance characteristics (physical and biochemical) on natural enemies including impact on the behavioral and physiological attributes of the natural enemies.

    c. Integration of the use of plant product extracts and natural enemies.

    d. Natural enemy nutrition provided by host plants.

2. Selectivity studies of biological and chemical toxicant effects on natural enemies:

Given the necessity for integration of chemical control measures (against either *Heliothis* or other pest species) with natural enemies in many production systems, it is paramount to understand the relative impact of these toxicants on *Heliothis* and its natural enemies. The following topics are essential to this understanding:

a. Comparative toxicity of biological and chemical toxicants to *Heliothis* and its natural enemies.
b. The potential for development of resistant biotypes of natural enemies.
c. Standardization of the techniques involved.

Inaugural Session

The Relevance of the Workshop to India

*M. V. Rao**

On behalf of the Indian Council of Agricultural Research and on my own behalf, I welcome you all to this International Workshop on Biological Control of *Heliothis*. I am deeply honored to address this distinguished gathering on this auspicious occasion of the Silver Jubilee celebrations of the Far Eastern Regional Research Office (FERRO) of the USDA Office of International Cooperation and Development (OICD) and the Indian Council of Agricultural Research (ICAR).

This is the second international workshop on *Heliothis*; the first one was held at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in November 1981. I hope this second workshop will take stock of the progress that has been made since 1981 and suitably plan future strategy for control of *Heliothis*.

This workshop is convened at an appropriate time. In recent years, developments in pest management have shown the importance of and need for developing nonconventional methods of pest control to complement chemical control methods. Excessive use of chemicals has led to (1) problems in food and fodder production because strains of pests resistant to pesticides have developed; (2) outbreaks of formerly minor pests, which are now assuming major status because their natural enemies are being destroyed; and (3) environmental pollution, which is affecting human health.

These problems have arisen not only in India but elsewhere as well. The pyrethroids have been indiscriminately used in the cotton fields in Andhra Pradesh in the last few years, with the result that the white fly (*Bemisia tabaci*), which is not controlled by these pesticides, has become serious and is threatening cotton cultivation in that state. The recent Bhopal tragedy and the insistent reports that we have received from all over the world about people dying due to misuse of pesticide, force us to search for alternative avenues to pest control.

Indiscriminate popularization of cropping systems without taking into consideration the pest complexes has created problems also; for example, *Heliothis* is reported to be responsible for losses in cotton and pulses in

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northwestern India. Similarly, *Pyrilla* in 1985 not only affected the sugarcane crop but several other crops, such as sorghum, pearl millet, maize, and even rice.

Besides the side effects of pesticides, the quality of pesticides is itself a problem in several countries. High prices, poor quality, and nonavailability when pesticides are most needed, are some of the problems that confront farmers.

Intensive agriculture has brought in its wake challenges of pests and diseases. This demands considerable efforts to control pests that are frequently appearing in epidemic proportions which no single control measure can adequately combat, and damage is colossal.

Scientists have evolved new strategies, and modern technologies including introduction of new seed varieties, coupled with adequate inputs—have brought forth a revolution in food production, but, I must hasten to add, this is not sufficient. Although at the moment the world as a whole has a surplus of food grains, hunger and starvation still exist in some areas. Some countries have successfully achieved sufficiency in food grains, yet at the same time there are great shortfalls in other countries. It is relevant, therefore, to develop strategies to further intensify and increase agricultural production.

In recent years, *Heliothis* has become a pest of worldwide importance. Highly polyphagous and cosmopolitan in occurrence, this pest is known to damage 60 cultivated crops, besides at least 67 other host plant species distributed in Asia, Australia, and Africa. In India, an annual loss of U.S. $ 300 million is estimated to be caused by this insect in pigeonpea (redgram or *arhar*) and chickpea (gram or *channa*) alone. There are other crops such as cotton, other legumes, and vegetables such as tomato, where damage by this insect is also severe.

In India, *H. armigera* (Hbn.) is a limiting factor in pulse production often causing total crop loss. It has been estimated that an average infestation of one larva per plant of pigeonpea can cause a yield loss of 1015 kg/ha in Karnataka state. In sorghum, yield losses of 18 to 26% have been reported in Maharashtra, while in cotton in Madhya Pradesh, losses of 41 to 56% occur. In horticultural crops such as tomato, yield losses of 40 to 50% are reported from Tamil Nadu.

While costly inputs such as insecticides may be helpful in controlling the damage by *H. armigera* in irrigated systems where crop productivity may justify such inputs, dryland systems which mostly grow pulses require a cheap but effective method of *Heliothis* management. It is imperative that biological control be given an increasingly important role to play in controlling this pest, as an important ingredient of the integrated approach to pest management. Though biological control is safe, economical, and durable, its full potential still remains largely unrealized.

Integrated pest management is critical to our efforts to reduce crop losses. It combines the use of resistant or tolerant varieties, suitable agronomic practices, need-based application of systemic and nonsystemic pesticides, and biological control. Choice of appropriate multiple and intercropping sequences, intensive study of pests, survey and surveillance, forecasting, and an infrastructure to take remedial measures should all form a package in our battle against *Heliothis* and other pests.

The first significant success in controlling pests through biological means was achieved at the suggestion of C.V. Riley of California, in 1888. The beetle, *Rhodalia cardinalis* (Mulsant) was introduced to control cottony-cushion scale, *Icerya purchasi* (Maskell) on citrus. By now, about 110 pests in 60 countries have been controlled by biological means. Biological control has the advantage that once established, it is self-perpetuating, and no further expenditure is involved.

To organize, promote, and coordinate the biological control work in our country, the ICAR has launched a massive All India Coordinated Research Project on Biological Control of Crop Pests and Weeds. Its main center is located at the Indian Institute of Horticultural Research (IIHR), Bangalore, and 15 cooperating centers operate in different agroclimatic zones of the country. The Directorate of Plant Protection (India) also has a well-established program with more than a dozen centers around the country.

Each cooperating center of the ICAR project has a major role to play, depending on the specific research needs of the region, in promoting efficient use of biocontrol agents as part of an integrated approach to pest control. The overall progress of work under the project has given a new dimension to biological pest control, making full use of such bio-agents as existed in nature and at the same time testing exotic species of natural enemies to suit the specific ecosystem. I am happy to note that we are not far from initiating "biological factories" for mass multiplication and release, either commercially or through governmental agencies, in the farmer's field.

In recent years, pathogens infecting *H. armigera* have been reported in several parts of India. They include nuclear polyhedrosis virus (NPV), cytoplasmic polyhedrosis virus (CPV); and granulosis virus (GV); one bacterium; two fungi; two protozoans; and one nematode. Extensive studies have been made on the pathogenicity, mass production, storage stability, field efficacy, and safety of NPV of *H. armigera*. NPV has been successfully used for the control of the semilooper in castor. Similarly, field studies conducted have indicated that the pest can be effectively suppressed by NPV when it occurs on chickpea. Since the pathogen is safe to nontarget organisms and is highly effective against the pest, its use in the management of the pest is likely to increase.

We hope, therefore, that this workshop will play a catalytic role in propagating practical biological methods of *Heliothis* control, and realistic and workable recommendations will be developed. The distinguished scientists here should give thought to:

1. Establishing indigenous enemies of *Heliothis* spp., and their propagation and release.

2. Developing effective and practical procedures which are also economically acceptable for receipt, quarantine and release of natural enemies of *Heliothis*.

3. Procedures for surveying, conserving, and augmenting effective indigenous natural enemies of proven merit for use under different agroecosystems.

4. Standardizing formulations of the promising indigenous insect pathogens, particularly NPV, for controlling *Heliothis*.

5. Planning biocontrol strategies for different ecosystems, including predicting both pest and natural enemy populations, so timely release of enemies can be undertaken by the farmers.

From the agenda of the workshop, I note that the participants will devote 5 days to a single insect complex that has assumed global status as a major pest, concentrating their discussion on a single topic: biological control—increasing the effectiveness of natural enemies. I am glad to find that there is adequate emphasis on and broad coverage of various aspects of this topic, particularly of recent trends in biological control.

I am sure that with an interdisciplinary research approach the distinguished workers who have assembled here will be able to probe deeply and unravel the mysteries of this insect and its control. We are fortunate to have with us distinguished scientists from India and abroad to interact closely during this workshop. I earnestly believe that, based on their deliberations, they will bring forward appropriate recommendations for the benefit of both the farmer and the research worker to tackle the menace of *Heliothis*.

Heliothis: Need for International Collaborative Research on Biological Control

R.D. Jackson, E.G. King, and *E.F. Knipling**

The main objective of this workshop is to review, analyze, interpret, and synthesize scientific knowledge on the biological control of *Heliothis*. We are defining biological control as the development and promotion of management tactics to improve the effectiveness of natural enemies for suppressing *Heliothis* populations.

The genus *Heliothis* Ochsenheimer, consisting of more than 75 species or subspecies (Todd 1978), includes some of the most important insect pests in the world. Those which have attained pest status are generally distributed widely and are highly polyphagous. These pests are called many names: corn earworm, bollworm, tomato fruitworm, podworm, tobacco budworm, etc. Our colleagues in the USA believe that it is inappropriate to call *H. armigera* (Hbn.) the American bollworm, when this insect is considered an Old World pest. However, recent evidence reveals that *H. armigera* and *H. zea* (Boddie) are capable of interbreeding (Laster et al. 1985). So, in fact, what we have is an international bollworm problem, with *H. armigera* achieving major pest significance in India, China, Southern Europe and Asia, Australia, USSR, and Africa, and *H. zea* being a major pest on the American continent. Other species such as *H. virescens, H. punctigera, H. viriplaca, H. assulta* and *H. peltigera* are also pests, but they are more limited in their geographic distribution.

We may ask ourselves, "Why is it that certain *Heliothis* species are such major pests? Is it simply because they attack fruiting structures of the plant? Or is it because they attack some of our most important food and fiber crops such as chickpea, pigeonpea, maize, sorghum, tomato, and cotton?" These pests are typified by being highly mobile, highly fecund,

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multivoltine, and voracious in their feeding; they also have a propensity for gaining resistance to insecticides.

Annual losses to *Heliothis*, worldwide, are estimated in the billions of dollars. In the USA alone, *H. zea* and *H. virescens* cause damage of about $1.25 billion annually; and this damage occurs in spite of control measures. Reports from India indicate that annual damage to chickpea and pigeonpea alone is U.S. $200 to $300 million annually. Such damage could easily be more than double if estimates from other crops attacked by *Heliothis*, such as cotton, maize, sorghum, and tomato, were included.

So, *Heliothis* species are truly a global problem and it is appropriate that this first international meeting on their biological control be held in India. India was the site of the first "International Workshop on *Heliothis* Management", sponsored by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at the center in Patancheru. An outgrowth of this workshop was the formation of the International *Heliothis* Biological Control Work Group within the International Organization of Biological Control of Noxious Pests and Weeds. This work group was instrumental in suggesting "Biological Control of *Heliothis*" as a topic for celebration of the Silver Jubilee of Cooperative Agricultural Research between the Indian Council of Agricultural Research and the Far Eastern Regional Research Office of the Office of International Cooperation and Development, U.S. Department of Agriculture.

Biological control is a cornerstone of integrated pest management, and the contributions of predators, parasites, and pathogens in the regulation of *Heliothis* populations are well recognized. This workshop is modeled around this appreciation, beginning with Subtopic I: "Measuring and modeling the effect of natural enemies." Subtopic II, "Distribution of *Heliothis* and their natural enemies and host plants," will describe our resource base, including an "assessment of opportunities for establishing new natural enemies." Because natural enemies often do not maintain *Heliothis* populations and consequent damage below "acceptable" levels, we must seek means to increase their effectiveness. One means is through "Exploration, importation, and establishment of new (and perhaps more) effective natural enemies of *Heliothis*," which is presented in Subtopic III. Subtopic IV reviews the latest technology for "Increasing the effectiveness of natural enemies" by enhancing their ability to reduce pest populations within a defined area. Increasing natural enemy effectiveness may be achieved by interplanting other species as refugia for natural enemies, providing shelters for parasites and predators, using behavior-modifying chemicals to simulate high host densities, providing host/prey or other supplemental food, or propagating or culturing of natural enemies. These natural enemies or their toxins (pathogens) may be released or applied on a

field-by-field or area-by-area basis. Finally, Subtropic V recognizes the need for "integration of biological control into crop production systems," treats other control approaches, including cultural practices, host-plant resistance, and chemical methods relative to their interaction with and strengthening of biological control. Certainly, it is recognized that for some crops the profit margin is so low that biological control, host-plant resistance, and cultural control may be the only management tactics economically feasible to use. Additionally, these tactics probably are less damaging to the environment than other control methods. Where therapeutic measures such as insecticides are necessary and yield positive monetary returns that exceed or equal those realized from alternative technologies or no control, these measures should be modified to achieve an additive effect, not simply to replace one mortality factor with another.

One of us (Knipling, 1979) has advocated the management of *Heliothis* populations on an areawide basis instead of the present defensive strategy of managing them on a field-by-field basis. Certainly, present strategies have reduced the *Heliothis* problem. Nevertheless, these populations remain at threatening levels year after year. Dr. Knipling theorizes that it may be possible to maintain *Heliothis* populations below significant damage levels on most or all crops at costs that would be only a fraction of the total costs that farmers now expend to reduce losses on high-value crops.

Population management, regardless of the strategy, requires coordinated action by individuals on an areawide basis. The size of the area is (should be) determined by the mobility of *Heliothis* and mobility of a predator or parasite if these are effective suppressants. Certainly, the origin and contribution of moths moving long distances (migration) to local *Heliothis* dynamics must be determined before population management is considered a fully viable option. Available evidence indicates that *H. zea* and *H. armigera* are capable of moving long distance each year.

Advances have been made on strategies for effective management of *Heliothis* populations. Laster (1972) reported successful hybridization of *H. subflexa* (Guenee) females and *H. virescens* (F.) males. Hybrid males were sterile, but hybrid females reproduced when crossed with *H. virescens* males. Further, sons of the hybrid females were sterile, but daughters were fertile when crossed with *H. virescens* males. This backcross sterility has persisted indefinitely in subsequent generations. These backcross moths have been reared on a large scale (King et al. 1985) and released on St. Croix, U.S. Virgin Islands, where they suppressed a feral *H. virescens* population (USDA, Agricultural Research Service, 1985). Efforts are now ongoing to achieve hybrid sterility in *H. zea* (Boddie) by crossing it with other species in the *Helicoverpa* complex (Laster et al. 1985). Since *H. zea* and *H. armigera* are obviously so closely related, achieving hybrid sterility in one species may lead to development of hybrid sterility in the other.

Another method of genetically altering moths involves the use of substerilizing dosages of irradiation, where the F_1 progeny are more sterile than the treated parents. So, in the event that hybrid sterility is not achieved in *H. zea* or *H. armigera*, then inherited sterility remains a viable option for population suppression. Another strategy for population suppression involves manipulation of host plants or suppression of *Heliothis* on noncultivated host plants when the insect density is low (reduced) and restricted to a limited area. For example, in the Mississippi River Delta area of the USA, early season populations (F_1) *Heliothis* are largely restricted to noncultivated host plants along field margins and roadsides. This early season habitat is less than 5% of the total agricultural area. Suppression of *Heliothis* at this time would be less expensive and less harmful to the environment than with repeated and widespread applications of insecticides after the crops have been planted (Knipling and Stadelbacher 1983). Removal of early-season, noncultivated host plants through mowing or herbicide, and application of microbials (*Heliothis* nuclear polyhedrosis virus) has been demonstrated in small plots as viable suppression tactics for *H. zea* and *H. virescens* (Stadelbacher 1985).

Propagation and release of one or more selective parasites on an areawide basis is considered a viable population management strategy. If we accept the premise that self-perpetuating populations of a given parasite have significant regulatory effects on *Heliothis* populations, we can assume that an augmented parasite population would have a greater effect on the dynamics of the host population. An example of a selective parasite is the solitary parasite, *Microplitis croceipes* (Cresson). This braconid is the most prevalent, and perhaps most important, parasite attacking *Heliothis* in the USA. Rates of parasitism by this braconid often exceed 50% in early-season, noncultivated host plants (Stadelbacher et al. 1984) and 30 to 50% in cotton fields in spite of insecticide applications (King et al. 1985). Higher than expected levels of larval parasitism in cotton have been attributed to reduced insecticide usage in general, and the relatively recent use of more selective insecticides, viz., pyrethroids. Powell et al. (1986) demonstrated that this braconid is relatively tolerant of pyrethroids. Monitoring of adult male populations of *M. croceipes* may be imminent, as the presence of a sex pheromone from female wasps has been demonstrated (Powell and King 1984). Moreover, *Heliothis* larvae parasitized by *M. croceipes* have been shown to move less and feed less than unparasitized larvae. Consequently, about 40% less damage occurs to cotton fruiting structures when the larvae are parasitized (Hopper and King 1984). A procedure for large-scale rearing of *M. croceipes* is being developed for testing augmentation effects on an areawide basis. However, utilization of this approach depends on development of mass rearing technology and demonstrated effectiveness of the suppressive capability of this parasite.

In conclusion, we take the position that suppression of *Heliothis* on an areawide or regional basis may be a viable option. Because long-range dispersal may be characteristic of species such as *H. zea* and *H. armigera*, it is essential that this phenomenon be elucidated and the origins of migrating populations be identified. Moreover, tests will be required and are likely to require huge resources and coordination by several agencies. Such experiments have associated high risks, but this is axiomatic, regardless of the field of science involved and the nature of the experiment. In view of the worldwide economic importance of *Heliothis* and continued environmental concerns caused by insecticide applications, the risks seem acceptable. The risk of species of *Heliothis* becoming highly resistant to present insecticides and suitable substitute materials not being available should be of far greater concern than high-risk experiments.

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The Role of Biological Control in Pest Management in India, Emphasizing *Heliothis* spp.

*K.S. Kushwaha**

I consider it a great privilege to address this learned audience at the inauguration of the Workshop on Biological Control of *Heliothis*. The problems of pest management have become more complex as we have shifted our consideration from single-species populations to multi-species systems, i.e., biotic communities and complete ecosystems. In the present context, let us consider the tactical adaptations of *Heliothis* spp. that have made their management difficult. The broad range of host plants sustains *Heliothis* populations throughout the year. Their geographical distribution, unpredictable occurrence, puzzling regional variation in host range, host preference, and host crossover merit study at an international level. The technology of management packages that combine insecticides, biological control agents, resistant varieties, and cultural practices makes it necessary to have "supervised" anti-pest operations at the farmers' level in a developing country like India.

DISTRIBUTION AND STATUS OF *HELIOTHIS* SPP.

Three species of the *Heliothis* complex, *H. zea* (Boddie), *H. virescens* (F.), and *H. armigera* (Hübner), are such devastating crop pests as to pose a global problem. *H. zea* and *H. virescens* are prevalent in the Americas, and *H. armigera* is distributed in all the other tropical and subtropical countries and causes severe damage in the semi-arid tropics. Traditionally, these species have received most attention as pests of cotton, particularly in the USA, where they cause losses estimated in the hundreds of millions of dollars.

In India, *H. armigera* is the dominant species; two other species are *H. peltigera* (Denis & Schiff) and *H. assulta* Guenée. At Udaipur, in Rajasthan state, studies on life tables based on large field populations of *H.*

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armigera in major crop hosts have been carried out (Kushwaha et al. 1984). *H. armigera* is a major pest of chickpea, pigeonpea, tomato, maize, and sorghum, but it also is a serious pest of cotton. Besides these crops, it has been recorded on more than 100 other plant species (Bhatnagar et al. 1982). The continuous availability of host crops, often planted as mono-cultures, and the lack of crop rotation greatly contribute to maintenance of high population levels of *Heliothis* and their consequent damage to crops.

INDIGENOUS ENEMY COMPLEX OF *H. ARMIGERA*

Our ecosystems are naturally endowed with a rich enemy fauna, including microbial pathogens that must be identified, conserved, augmented, and manipulated to advantage. Extensive field surveys were conducted, mostly in south India, during the 1960s, primarily by entomologists at the Indian station of the Commonwealth Institute of Biological Control (CIBC), Bangalore. These scientists published a comprehensive list of 37 species of parasites associated with *Heliothis* (Achan et al. 1968; Rao 1968) and subsequent investigations revealed 60 species (Rao 1974). Studies undertaken at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) since 1974 have identified 27 species of parasites from Andhra Pradesh, Maharashtra, and Karnataka states (Bhatnagar et al. 1982). Ten of the total identified species are relatively effective in regulating *Heliothis* populations (Table 1).

Table 1. Important parasites of Heliothis armigera *in India*

Parasite	*Heliothis* stage affected and percentage parasitized
Hymenoptera	
Braconidae:	
Bracon brevicornis Wesm.	Larvae, 3–6%
Ichneumonidae	
Banchopsis ruficornis (Cam.)	Larvae, 10%
Campoletis chlorideae (Uchida)	Young larvae, 10–80%
Enicospilus sp.	Old larvae, 6–11%
Eriborus sp.	Young larvae, 3–6%
Trichogrammatidae	
Trichogramma chilonis Ishii	Eggs, to 79%
Trichogrammatoidea armigera Nagaraja	Eggs, to 11%
Diptera	
Tachinidae	
Palexorista laxa (Curran)	Old larvae, 12–18%
Carcelia illota (Curran)	Old larvae, 4–16%
Goniophthalmus halli (Mesnil)	Old larvae, 18–20%

Sources: Achan et al. (1968); Manjunath (1972).

Studies on the role of mortality parameters in field populations of *H. armigera* at Sukhadia University, Udaipur, have revealed an overall parasitization by 13 parasitoids of up to 35.7% and mortality attributed to bacteriosis up to 10.5% in chickpea, 1981–84. The corresponding mortality in the tomato crop in farmers' fields at village Balechi adjoining Udaipur (1981–83) was 9.7% from parasitization by parasitoids and 25.1% from bacteriosis. The collective overall mortality (based on weekly field-collected larvae reared individually in the laboratory) from parasitoids and bacteriosis in larval and pupal stages is illustrated for one site (Figure 1) at the experiment station and a second site (Figure 2) in farmers' fields. Of the various parasitoids, *Campoletis chlorideae* Uchida is the only one that effectively regulates the pest population in the two crops (Figures 3, 4).

The All India Coordinated Research Project on Biological Control of Crop Pest and Weeds, with its multilocation centers, involving agricultural universities and national institutions, is striving to streamline the biocontrol dimensions for taxonomic, ecological and biological bases. This work has gained momentum through feedback from the Directorate of Plant Protection, Quarantine, and Storage, and the Indian station of the CIBC. Thus the current attitude appears to be favorable for biological control.

FIELD RELEASES OF PARASITES AND PREDATORS

The response of resident or an introduced exotic natural enemy to counteract a sudden increase in a *Heliothis* population may not be sufficient in all situations. Nevertheless, specific testing trials over large areas are needed to assess the future prospects of classical biological control involving introduction of exotic species. Nagarkatti (1982) has made a valuable contribution presenting available information on the use of biological control in *Heliothis* management in India. Under the regular schedule of periodic releases, the following parasites have amply demonstrated positive results in the cotton crop, particularly in Gujarat state (Anonymous 1983):

Egg parasites	*Trichogramma brasilienis* Ashm.
	T. achaeae Nagaraja and Nagarkatti
	T. chilotraeae;
Egg-larval parasites	*Chelonus blackburni* Cameron;
Larval parasites	*Bracon kirkpatricki.*

Also, the predator *Chrysopa* spp. is important as an egg predator.

In the area of natural enemy release, comparable yields were obtained from biological control and chemically treated plots. The cost of control for these two treatments was comparable also. Consequently, the Directo·

Figure 1. Ultimate adult population of *H. armigera* surviving mortality caused by parasitoids and bacteriosis; based on regular sampling of larvae in chickpea crop on the College Farm at Udaipur, Rajasthan, 1981–84.
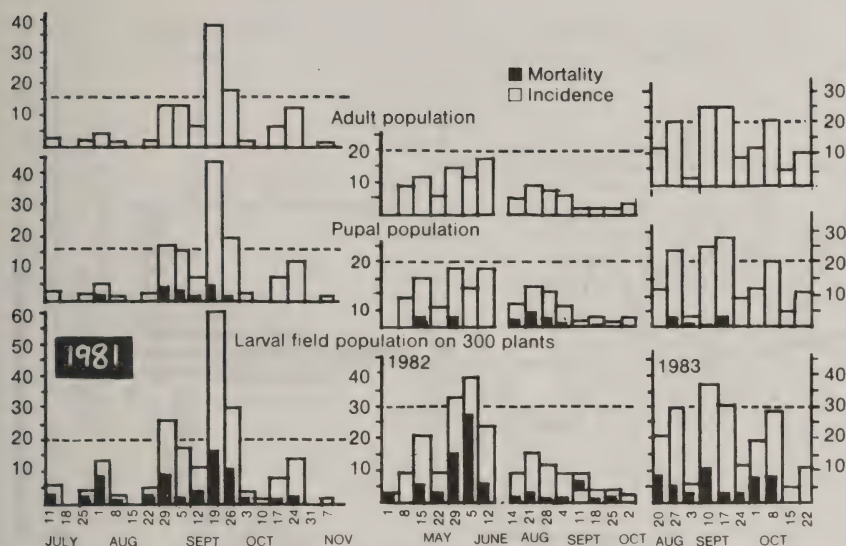
Figure 2. Ultimate adult population of *H. armigera* surviving mortality caused by parasitoids and bacteriosis; based on regular sampling of larvae in tomato crop in farmers' fields, village Balechi, adjoining Udaipur, Rajasthan, 1981–83.

rate of Plant Protection is organizing bulk production of *Trichogramma* spp. for supply to farmers.

FIELD USE OF PATHOGENS

Applications of nuclear polyhedrosis viruses (NPV) in the cotton crop in Gujarat state have effectively controlled *Heliothis*. Similar applications, in preliminary trials on chickpea effectively managed *Heliothis* populations. Yield in treated plots was 47% greater than in untreated plots. Commercial availability of this viral pathogen is being ensured for use by the farmers (Anonymous 1983).

Unfortunately, the naturally occurring bacterium, *Bacillus thuringiensis* Berliner, cannot be used on a field scale in some Indian states because of the potential effect on the silk industry. So research is needed to select strains less toxic to the silkworm (*Bombyx mori*) yet maintain toxicity against *Heliothis*.

EXOTIC PARASITES

The tachinid *Eucelatoria bryani* (Coq.) is now being released and evaluated for control of *Heliothis*. Other research on this parasite includes
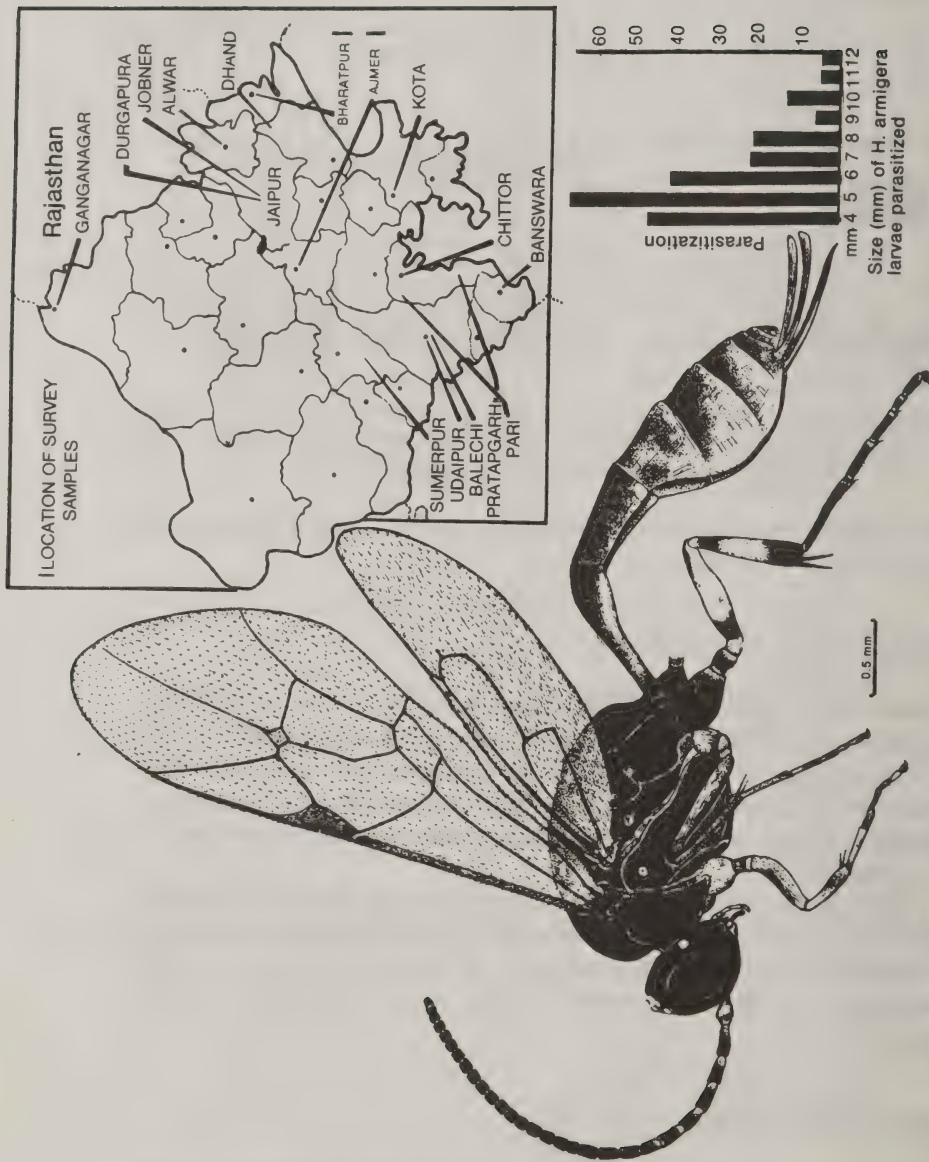
Figure 3. The major parasitoid, *Campoletis chlorideae* Uchida (adult), (Hymenoptera: Ichneumonidae) larval parasite: Parasitization preference (%) for size of host larvae, *H. armigera*.
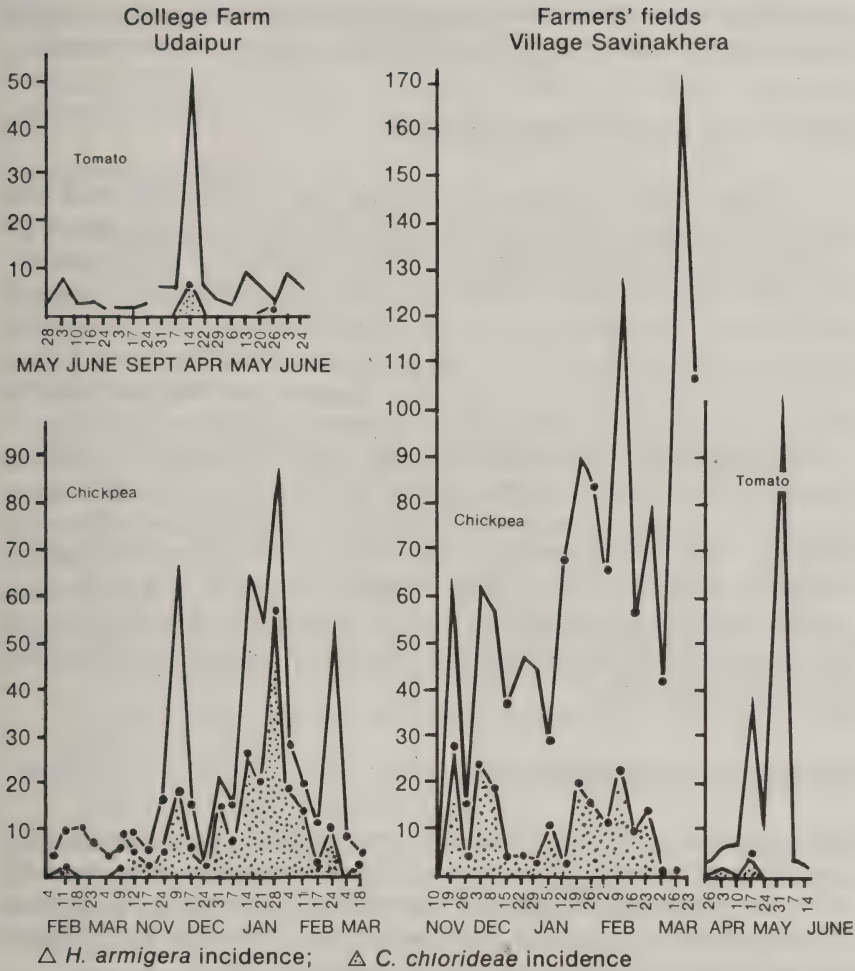
Figure 4. Relative incidence of *H. armigera* and its major parasitoid, *Campoletis chlorideae*, in chickpea (College Farm) and tomato, village Savinakhera, adjoining Udaipur, Rajasthan, 1981–82.

assessing the toxicity of selected insecticides. Other exotic parasites being evaluated include three larval parasites—*Cotesia* (= *Apanteles*) *marginiventris* (Cresson), *Chelonus texanus* (Cresson), and *Campoletis flavicincta* (Ashmead)—and the predator, *Chrysopa scelestes* Banks. It should be noted that in inundative releases of exotic species, the size of the founder population and genetic makeup of the species is important.

DeBach (1974) advocated a sustained and methodical approach to biocontrol ecology. It is most important to demonstrate experimentally the extent of control exerted by the various components of pest manage-

ment. There is a need to establish large-size, paired plots for comparison in field trials. All factors should be excluded except the one to be tested.

SELECTIVE USE OF INSECTICIDES

Use of insecticides to temporarily alleviate high *Heliothis* or other pest populations seems to be inevitable. However, the insecticides should be selected with care to minimize predator and parasite mortality. For example, cotton growing had to be discontinued in the Ord Irrigation Area of northwestern Australia because excessive pesticide use destroyed natural enemies as well as selected out resistant populations of *Heliothis* (Wilson 1974). Aerial spraying in some areas of Gujarat and Haryana states in India has also adversely affected natural enemy populations in cotton.

One insecticide, phosalone, has been reported harmless to natural enemies by Sukhoruchenko et al. (1977). Our laboratory trials at Udaipur have indicated that phosalone and endosulfan are relatively safe to the parasite *C. chlorideae* at 0.02% concentration (lower than the recommended 0.05%). Wilkinson et al. (1979) reported fenvalerate and permethrin (pyrethroids) as significantly less toxic to the parasite *A. marginiventris* and three predators of *Heliothis* spp. than the organophosphates sulprophos and profenophos.

CRITICAL CONSIDERATIONS

The egg parasites, *Trichogramma* spp., are considered of great potential in regulating *Heliothis* populations in spite of their apparent poor searching ability and preference for specific crop ecòsystems. The egg-larval parasite *Chelonus heliopae* Gupta and larval parasites *C. chlorideae* and *Eriborus* spp. are not amenable to mass rearing (Nagarkatti 1982).

C. chlorideae was shipped to the USA but proved incompatible with *C. sonorensis* for trials against *Heliothis* spp. Additionally, two egg parasites and the tachinid *Palexorista laxa* Curran successfully developed in *H. zea* (Manjunath 1972). Among indigenous Indian dipterans, the following were amenable to mass production and merit field evaluation: *P. laxa*, *Carcelia illota* Curran,. *Goniophthalmus halli* Mesnil, and *Peribaea orbata*.

In conclusion, it is important to remember that introduction of the Indian "mynah" (*Acridotheres tristis*) bird into Mauritius to control the red locust in 1762 marked the beginnings of what we presently identify as the field of biological control. This was also the first successful movement of a natural enemy from one country to another (Moutia and Mamet 1946). Finally, Swaminathan (1976) called for a greater rapport between

those who move society and those who move science and technology to achieve the ends we desire. The field of biological control has a long history and it is effective; however, its implementation will require cooperation between all parties.

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Measuring and Modeling the Effects of Natural Enemies on *Heliothis* spp. Populations

Introduction

W. Reed*

In this session we will examine the impact of natural enemies of *Heliothis*. Obviously it will be a rewarding session, given the quality of the participants. However, we should remember that in many circumstances we still have no accurate means of actually measuring areawide *Heliothis* populations. Such information should be basic to the consideration of biotic and abiotic effects on these populations.

We can count eggs and larvae on samples of individual host plants in the field and so monitor the progression of infestations on single crops, or even on a succession of crops, in an area. We can also set emergence traps in fields to monitor the quantitative emergence of moths resulting from such infestations. We can use life tables to develop an understanding of the relative importance of the various factors in the population dynamics of the pest and its natural enemies in the field. We can, but we seldom do! Most life tables recorded in the literature are based upon laboratory data rather than on field observations. Most population records are from single crops, with cotton entomologists restricting themselves largely to cotton and other crop entomologists restricting themselves to their target crops. Here in India, *H. armigera* has been recorded on 175 host plants, many of which are used as crops. I am sure that these records greatly underestimate the number of hosts on which *H. armigera* can and does feed. This complexity is probably the major reason why we do not have a paper from India in this section.

Counting eggs and larvae on so many host plants is an impossible task, so if we are to consider *Heliothis* populations across an area or region we must develop some quantitative monitoring system to measure area densities. The moth is the obvious stage to monitor, and we have imagined that we have been able to "monitor" moths through light traps and more recently through pheromone traps. Unfortunately, work at ICRISAT and other centers over the past few years has convinced us that light traps and pheromone traps cannot be relied upon to give direct and accurate, or even adequate, estimates of moth densities in an area. Thus, we still have a basic problem!

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We are all dedicated to the protection of our environment but most of us also want material benefits and comforts. The two aspirations are not always complementary. Insecticide use has undoubtedly contributed to our comfort, but misuse has been highlighted, particularly through the effects on population of *Heliothis* spp. There is little doubt that *Heliothis* outbreaks in some areas and crops, particularly on cotton, can be attributed to the destruction of natural enemies. However, we certainly cannot generalize that *Heliothis* spp. are unnecessary pests, which are the result of man's mishandling of pesticides. Here in India, the major grain legumes, pigeonpea and chickpea, have always suffered tremendous losses to *H. armigera*, in spite of very limited insecticide use in these crops and in the environment. Here the key appears to be that of population movement— the moths invade the crops in large numbers and the natural enemies do not. Dr. V.S. Bhatnagar's work, which will be referred to frequently in this workshop, has highlighted the fact that the quality and quantity of the natural enemy complex on *H. armigera* is strongly influenced by the plant host. In such a situation the natural enemy effects on areawide populations are obviously very complex. However, that is no excuse for not trying to quantify those effects. We will not enhance our credibility if we continue to · regard natural enemy effects as being desirable, but variable, unreliable and nonquantifiable. We must not expect farmers to rely on providence, for they require assured yields and profits.

Coaker (1959) put forward the theory that *H. armigera* was a major problem in Tanzania but not in Uganda, because in the former there was a hot dry season during which *H. armigera* was scarce, so its natural enemy complex was also reduced, whereas in Uganda, *H. armigera* could breed and feed all year, and the natural enemy complex stayed with it. That was an attractive theory, but I am not sure that there is, as yet, quantitative evidence for its support, largely because nobody works on a pest in areas where it is not a pest! There are so many areas of the world where one would expect *Heliothis* to be a pest but it is not, and no one knows why! I continue to regard *Heliothis* populations in most areas of the world as unexplained mysteries. Perhaps this session will help to clear some of the mystery. However, I am convinced that adequate explanations of *Heliothis* population dynamics will not be available until we learn more about the movements of the moths and of their natural enemies.

I would like to close this introduction with two comments that greatly impressed me. The first was by Prof. O.W. Richards in 1957, who commented, "I am often told that parasites and predators control pest populations but in almost all cases that I have seen it was the pest population that controlled the parasites and predators." The second was in this week, by Dr. E.G. King, who commented, "It is not the percentage of the pest population that is killed by natural enemies that is important, but how

many pest individuals survive to damage the crop." There is little doubt that *Heliothis* spp. are among the more difficult insects to tackle with biological control action, but that natural enemies are very important in their population dynamics. We still have much to learn!

Estimating the Abundance and Impact of Predators and Parasites·on *Heliothis* Populations

*Winfield Sterling**

ABSTRACT

Nonintervention describes the decision to rely on natural mortality for the control of pest populations in the absence of any intervention by man. The distinction between nonintervention and conservation, cultural control, biological control, etc., is based on whether or not man plays an active role in the process of pest control. Management decisions are discussed in relation to the concepts of sustainability and ecosystem restoration. Perhaps the most common decision made by pest managers is not to intervene in the affairs of pests or their natural enemies; in Texas cotton production systems, this decision is made about 95% of the time. Inaction levels, based on the density of key natural enemies, and action (decision) levels are available to aid in making decisions for boll weevils and *Heliothis* species to minimize the risks associated with decisions.

To establish the inaction levels for natural enemies, the methods used for estimating the abundance of both the pests and their natural enemies can be critical. A high research priority is suggested for calibrating various density estimation methods to absolute population estimates. Absolute estimates are needed for the construction of life budgets and for modeling. Presence-absence methods are a time-saving tool for making pest management decisions, especially when used in conjunction with sequential sampling. But pest management sampling is of limited value unless the true impact of both the pests and their natural enemies is known. Methods of use in determining the impact of natural enemies are outlined. Though no universally superior methods appear to exist, some techniques have distinct advantages for certain situations. For example, durable evidence is suggested for use if this kind of evidence remains at the end of the generation.

INTRODUCTION

As problem solvers, we have not done a very good job of finding ways to

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ameliorate the *Heliothis* problem without developing new problems. For example, the ecological backlash from overuse or misuse of chemical insecticides (van den Bosch 1978) is well known. But what will be the long-term impact of specific host-plant resistance mechanisms, or of cultural, genetic, or biological control tactics applied to *Heliothis* spp.? *Sustainability* of a tactic is one important measure of the value of that tactic. How will these various tactics hold up to the test of sustainability?

It can be argued that, in general, we are not much closer to sustainable solutions to the *Heliothis* dilemma than we were at the turn of the century. Insecticides have not really reduced crop loss to insects (Allman 1985), which is still about 20%—the same as in 1900. *Heliothis* are probably more abundant now than in the 1800s, due largely to resurgence resulting from insecticide resistance and the much greater standing crop of host plants (i.e., cotton, soybeans, sorghum, etc.).

Whether or not we agree with this scenario, it would be difficult to avoid the conclusion that *Heliothis* species are a continuing problem. Though many panaceas have been proposed and tested, *Heliothis* will continue to resurge unless we can increase the sustainability of control tactics employed. Hardin (1985) has suggested that when man intervenes in the functioning of ecosystems, he never does only one thing. Plowing the prairie to plant crops may result in increased soil erosion due to the exposure of the bare soil to wind and rain. Treating *Heliothis* with insecticides results in the development of resistance. Introducing high gossypol content into cotton lines for host-plant resistance may exacerbate cotton leafworm problems (Montandon et al. 1986). The mongoose, released into Jamaica and Puerto Rico for the control of rats in sugarcane fields there, has become a major reservoir and vector of rabies and a predator of chickens, ground-nesting birds, and waterfowl (Pimentel et al. 1984). For every action there is a reaction (to paraphrase Newton's third law of mass and force), and small changes in the ecosystem can have very large effects. Quick-fix panaceas to the *Heliothis* problem have so far not provided highly sustainable solutions.

But partial solutions exist that lend themselves to the sustainable suppression of *Heliothis* populations; one is to stop, or at least minimize, the killing of the pest's natural enemies. As DeBach (1974) stated, "Effective conservation of established natural enemies is absolutely essential if biological control is to work at all." Knipling (1979) also contended that the conservation of natural agents already present, permitting them to exert their normal regulating effects, should be the first goal of solving insect problems. To illustrate the importance of this concept, let's use a Texas example.
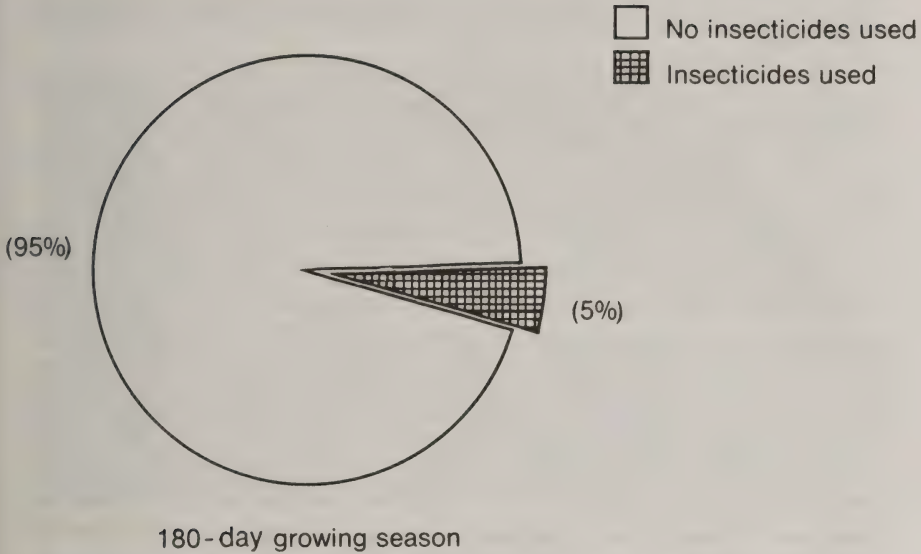
Figure 1. Insecticide use on cotton acreage in Texas, USA, over a 180-day growing season.

THE TEXAS EXAMPLE

In Texas, about 66% of the cotton is not treated with chemical insecticides during the growing season (TAES 1985). Viewed from a perspective of time, and considering that the cotton crop may require about 180 days from planting to harvest, Texas cotton is not being protected by chemical insecticides about 95% of the growing season (Sterling 1987) (Figure 1). Although cotton has recently been replaced by corn as the greatest crop user of insecticides in the USA, cotton still received about 16.9 million pounds (7.68 million kg) in 1982 (Adkisson 1986). We assume that other crops such as sorghum, wheat, and soybeans are protected by chemicals less than 5% of the time.

But how can this be? These crops are grown as monocultures and some theory suggests that lack of diversity leads to instability; thus it is reasonable to conclude that cotton is unstable. So, when pests attack, emergency actions such as the application of insecticides or inundative releases of predators or parasites seem essential to protect the crop. However, monoculture crops are not as unstable as theory suggests. Of course we can increase the instability by extending the length of the growing season with fertilizers and irrigation or by minimizing the influence of natural enemies of pests with insecticides, but basically many field crops are stable enough not to need continuous protection with insecticides. Of all the crop acreage in the USA, insecticides are used on only about 6%, and nonchemical means of insect control on 9% (Pimentel et al. 1978). This leaves 85% of the

crop area in the USA relying on the natural control of real and potential insect pests.

This is a tribute to the efficiency of natural mortality factors, which include the effects of predators, parasites, pathogens, competitors, weather (wind, rain, temperature, humidity, etc.), and natural plant chemicals that exhibit toxicity, deterrence, or digestibility effects on potential pest species. Native polyphagous predators often contribute regulating— and irreplaceable—mortality to pests of crops. Some natural enemies such as spiders are highly vagile (Dean and Sterling 1985) and capable of rapidly colonizing young crops. Predacious arthropods can be very efficient in preventing outbreaks of pests (McDaniel and Sterling 1982; McDaniel et al. 1981; Sterling et al. 1984). If pests are scarce in the crop, credit may also be given to natural mortality impinging on the pest before it colonizes the crop; i.e., while it remains on some reservoir host plant. Thus, claims that natural enemies are having limited impact on pests because pests are either very abundant or very rare in the crops, may be spurious and should be examined critically, since population regulation may occur outside the crop boundaries.

SUSTAINABILITY

Can pests become resistant to biological control (BC) agents or host-plant resistance (HPR) mechanisms? Nature is full of evidence of insects becoming resistant to their natural enemies. Choose any insect and evaluate the ways in which it defends itself against its enemies. No insect is totally defenseless. It can move rapidly, fight back, hide, utilize defensive chemicals, have eyespots or spines, be unpalatable, etc. It is unlikely that these defenses are due to random chance. The presence of defensive mechanisms is evidence that the fitness of the species is increased due to these mechanisms. If we find this evidence acceptable, then we must conclude that insects can develop resistance to their natural enemies. The key question then becomes: what is the rate of development of resistance and is it high enough to interfere with the control tactic? There is apparently no hard evidence suggesting that *Cactoblastis* sp. has lost its effectiveness against the cactus plant in Australia even 60 years after its introduction. *Rhodalia cardinalis* (Mulsant) has also apparently maintained its effectiveness against the cottony-cushion scale (*Icerya purchasi* Maskell) in California for about 93 years.

For comparison, a HPR tactic such as the introduction of wild Texas grape rootstocks for the development of resistance to the grape phylloxera (*Phylloxera vitifoliae* (Fitch)) has been a sustainable solution for 115 years in Europe. On the other hand, the evolution of adapted "biotypes" or

"strains" that are unaffected by HPR factors may require <7 years (Gould 1986). Some groups of insecticides, such as the organophosphates, have a sustained efficiency against the boll weevil (*Anthonomus grandis* Boheman) of about 30 years. On the other hand, organochlorine resistance was evident in 14 species of pests of cotton in only about 9 years (Newsom and Brazzel 1968). Perhaps we can conclude that some tactics, such as biological control, may have greater overall sustainability than others, but the issue is confusing. For example, how do we account for the examples of biological control, HPR, genetic control, etc., that were attempted but not completely successful? There is a paucity of information regarding the sustainability of these tactics.

No method of direct control that overlooks the root causes of rise to pest status will be permanent (Chant 1966). Of course in evolutionary time few things are permanent, and permanence is probably an unrealistic goal in pest management. However, as these examples show, sustainability on an ecological time scale has been clearly demonstrated to be possible.

NONINTERVENTION OR CONSERVATION?

The process by which wild natural enemies regulate pests at endemic densities should result in a high degree of sustainability on an ecological time scale, especially if the two groups of organisms have evolved in response to mutual selection pressures. Continued sustainability is likely since, as the pests evolve better defenses, natural enemies also become better adapted to exploit the pest. Adaptation and counteradaptation of natural enemies and their prey should maintain the overall efficiency of natural enemies while also insuring that the pests do not become extinct. But if man does not intervene in the activities of natural enemies, this lack of action is not conservation and should be labeled by some other name. Conservation implies that man is playing an active role in the process by which natural enemies control pests. The process of relying on natural control can be labeled *nonintervention* to distinguish it from true conservation, where man intervenes by manipulating natural enemies through the use of reservoirs. Nonintervention is the management decision and natural control is the process (Figure 2).

Through the traditions handed down from Aristotle and Darwin, the naturalist philosophy still dominated into the 1880s. But with the introduction of paris green, an arsenical insecticide, man obtained a powerful tool capable of massive intervention in the affairs of pests and their natural enemies. It is likely that the advent of paris green and the equipment to deliver it started the rapid and dominating growth of the interventionist paradigm. All of the interventionist tactics relate back to this
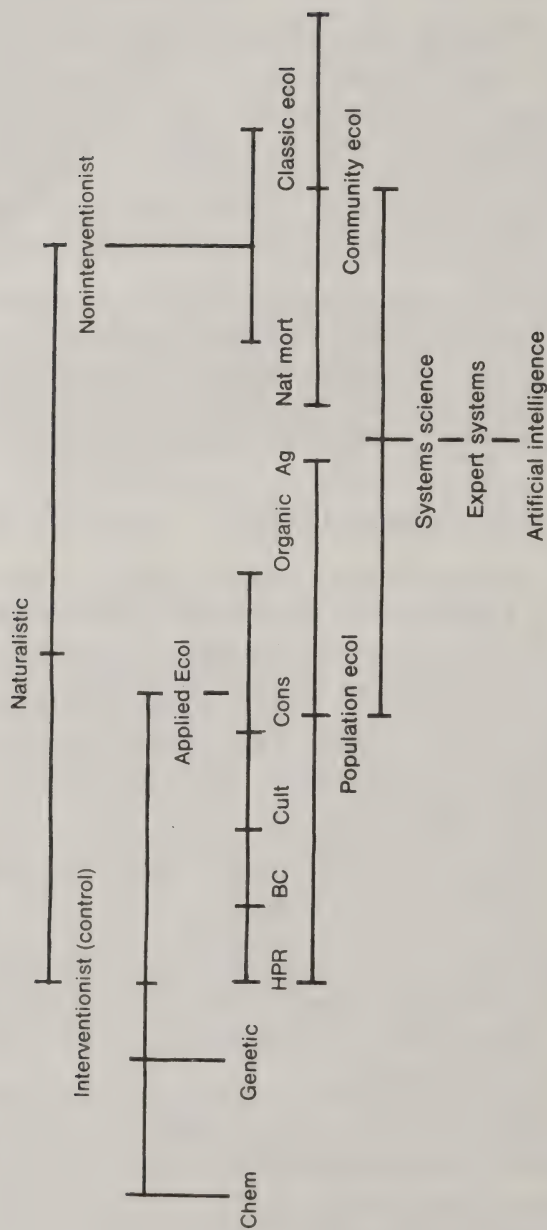
Figure 2. The evolution of man-insect paradigms.

Ecol = ecology; chem = chemicals; HPR = host-plant resistance; BC = biological control; cult = cultural; cons = conservation; organic ag = organic agriculture; nat mort = natural mortality; classic ecol = classical ecology.

important split away from the naturalistic paradigm. Some were modified through the applied ecology route. Biological control, cultural control, genetic control, and host-plant resistance are tactics which utilize varying degrees of the fundamentals of applied ecology. On the other hand, little ecological theory has been used in developing chemical control tactics (van den Bosch 1978).

Nonintervention continues the naturalist tradition. Natural mortality modified for man's benefit is biological control. Natural control without man's intervention leads us to the main subject of this paper, i.e., natural enemy impact and sampling.

NATURAL ENEMY IMPACT AND SAMPLING

Impact Analysis

Evaluating the impact of predators is complicated when predators consume the entire prey so that no durable evidence of predation remains after the act is completed. Since the act of predation may be completed in a relatively short time, and since predators often spend only a small part of their circadian activities actually feeding, the probability of our observing the act of predation under natural field conditions can be very low. Thus, many methods have been developed (DeBach et al. 1976, Grant and Shepard 1985, Kiritani and Dempster 1973, Pedigo et al. 1983, Southwood 1978) to increase the probability of detecting and evaluating predation (Table 1). There is no universally superior approach, but certain techniques have distinct advantages in certain situations. But, as a rule of thumb, experimentation with predators in natural situations permits more realistic understanding (Pedigo et al. 1983).

Table 1. Outline of methods for analyzing the impact of predators

I. Exclusion (using islands, fences, cages, etc.)
    A. Prey remain but all natural enemies are excluded to determine the impact of all mortality agents as compared to the check (DeBach 1964)
    B. Prey remain with selected natural enemies excluded (Pedigo et al. 1983)
II. Elimination
    A. Insecticidal check (DeBach 1964)
    B. Biological check (Fleschner 1958)
    C. Insecticide trap (DeBach 1964)
    D. Removal (manual or mechanical) (Fleschner 1958)
III. Liberation
    A. Field collections and release (Leigh and Gonzalez 1976)
    B. Rear and release (including cohorts for life tables)
        1. Selective placement (Nuessly and Sterling 1986, unpublished).
        2. Inundative releases of prey (McDaniel and Sterling 1979)
    C. Introduction for classical biological control (DeBach 1974)

IV.   Attraction
    A.   Trap plants
        1.   Plants with high nectar concentrations (Agnew and Sterling 1982)
        2.   Plants attractive to natural enemies (Stern et al. 1964)
    B.   Kairomones (Lewis and Nordlund 1985)
    C.   Supplementary feeding (Hagan et al. 1971)
V.   Confinement
    A.   Cages (Ridgway and Jones 1968)
    B.   Islands (Wilson and Simberloff 1969)
    C.   Barriers (Risch and Carroll 1982)

VI.   Observation
    A.   Predators with prey or in act of predation (Kiritani et al. 1972)
    B.   Field counts of predator and prey for correlations (Grant and Shepard 1985)
    C.   Feeding behavior in cages or observation chambers (including the components
        of predation i.e., feeding rate, searching area, etc.) (Holling 1961)
VII.   Labeling
    A.   Radioisotopes (McDaniel et al. 1978)
    B.   Rare elements (Pedigo et al. 1983)
    C.   Dyes (Hawkes 1972)

VIII.   Prey detection (feeding trace from natural conditions)
    A.   Gut analysis (Sunderland 1975)
    B.   Serological analysis (Boreham and Ohiagu 1978)
    C.   Fecal examination (Chapman et al. 1955)
    D.   Chromatography (Kiritani and Dempster 1973)
IX.   Dissection (Cate 1985)
X.   Rearing from host (van Driesche 1983)

XI.   Simulation
    A.   Mathematical models (Stimac and O'Neil 1985)
    B.   Computer simulations (Hassell 1978)
XII.   Durable evidence
    A.   Spider prey in web or on soil surface (Nyffeler et al. 1987, unpublished)
    B.   Evidence remaining in fruit, galls, or stems (Sterling et al. 1984)
    C.   Prey remains (Phillips and Barber 1933)

XIII.   Trapping emerging natural enemies (Southwood 1978)
XIV.   Sounds of predators feeding (California-Arizona Farm Press 1986).
        Uses very sensitive microphones that can detect the different sounds of predators
        and their prey during the act of predation.

The outline presented in Table 1 emphasizes the experimental processes rather than the experimental tools as a means of synthesizing information on the available choices of methods for use in impact studies. Predator efficacy can also be evaluated by identifying the relative importance of individual species or life stages of a species by categories such as (1) key predators, (2) secondary predators, (3) occasional predators, (4) possible (or potential) predators. The abundance of a key predator provides predictive value of prey abundance and also provides a level of irreplaceable mortality which tends to lead to prey regulation (example is

red imported fire ants). If the prey is a pest species, the key predator will tend to regulate the pest at densities below the economic threshold or the action level. There is a temptation to expect a key predator to be perennially occurring as in the Smith and van den Bosch (1967) definition of a key pest. But viewing predators on a time-space-abundance continuum shows no single predator species will always be present at the appropriate time, in the right place and in sufficient numbers, to always regulate prey abundance. But a key predator would be more likely to be present in the right place, in sufficient densities, at the appropriate time to effect prey regulation than a secondary predator.

Exclusion studies, either chemical or mechanical, are designed primarily to answer the question: does pest regulation by natural enemies occur? Conclusions made from exclusion studies are often limited to the generalization that natural enemies as a group have some impact on prey species abundance. Most insects are limited to a major extent by natural enemies, so exclusion studies provide little new information except to add another species to the list of animals limited by natural enemies.

A more critical goal may be to determine the mechanisms of pest population regulation. Learning *how* to predict the impact of natural enemies is a much more important objective than continuing to establish the fact that natural mortality exists. The impact of natural enemies will change in time and space, so an exclusion study has little value in predicting mortality elsewhere and later. "Key" natural enemies and their individual and mutual impacts on prey-host populations must be identified before there is much chance of accurately predicting their impact. Pertinent questions to be answered are: What are the key natural enemies? Are the important natural enemies really known; i.e., are there some feeding links in food webs that are unknown? What is the real impact of these natural enemies? What are the feeding rates of the key natural enemies on the pest species? What factors affect the mortality rate imposed by the natural enemies on the pest? Research protocol might follow the steps outlined in Table 2.

Other Methods

Many methods are available for evaluating the impact of natural enemies (Table 1). For example, for identifying feeding links that may have been missed by other methods, the release of large numbers of prey radiolabeled with ^{32}P has proven very effective. In cotton, several previously unknown feeding links were identified using this technique (McDaniel and Sterling 1982). Arthropods previously thought to be relatively innocuous were found to be likely candidates for designation as "key" predators. Visual observation and other methods had failed to identify the cotton fleahopper

[*Pseudatomoscelis seriatus* (Reuter)], the red imported fire ant (*Solenopsis invicta* Buren), the winter spider [*Chiracanthium inclusum* (Hentz)], or the black and white jumping spider [*Phidippus audax* (Hentz)] as important predators of *Heliothis virescens* (F.) eggs. Using the same ^{32}P technique to label the various larval instars of *Heliothis*, a very high level of mortality (over 99% real mortality) was observed.

One of the main problems with impact studies for either parasitoids or predators is the misidentification of the mortality agent. Rearing parasitoids from hosts held with plant material can result in misidentifications, since other animals may be present in the plant material besides the host and parasitoids. Dissection of parasitoids from the host generally results in more accurate identifications (Cate 1985). The major limitation of this technique is that the prey is removed from exposure to other mortality agents when it is collected. This method will thus tend to underestimate total generation mortality of the prey.

In studies of predation, one common error comes from secondary predation; ^{32}P, rare elements, dyes, or prey antigens may be detected in a top predator that had consumed an intermediate predator that had in turn consumed the labeled species. Or electrophoresis may show prey enzymes in the predator's gut, due to a similar sequence. Errors can also creep into observational methods. For example, the identification of suspected prey being carried to the colony by ants may be in error if the prey had already died from some other cause and the ants are really hauling carrion. To avoid possible misinterpretation of data and other difficulties in natural impact studies, the direct and indirect methods reviewed by Kiritani and Dempster (1973) should be consulted.

The release of laboratory-reared cohorts of animals in the field is a

Table 2. Research steps for identification and use of native natural enemies

1. Conduct faunal studies in the crops to be managed.
2. Identify the predatory species.
3. Identify the feeding links in the food webs of these key organisms.
4. Determine the impact of the natural enemies on the key pests.
5. Identify the key natural enemies regulating or suppressing the key and secondary pests.
6. Determine the action levels (treatment thresholds) and the inaction levels of the key natural enemies.
7. Develop sampling techniques with a known level of reliability for making decisions to intervene or not to intervene.
8. Develop predictive, interactive computer models of the key pests and natural enemies and the host crop.
9. Use the model to generate dynamic action and inaction levels and to provide decision aids and information (videodisc could be used here).
10. Refine the models with mechanistic subroutines, expert systems, and artificial intelligence.

simple but powerful method for predator studies. The primary advantage over surveys of natural populations is that supplies of laboratory-reared pests are usually more dependable than the fluctuating populations in nature, which often limit field studies. Also, the researcher has the option of changing variables such as pest density or dispersion in the experimental design. The changes in behavior of reared insects when released in nature can, however, be a major limitation of this technique.

Durable Evidence

Evidence that remains after all individuals in a generation or cohort have died constitutes durable evidence. If this type of evidence remains, this can be an excellent method for identifying mortality (Sturm and Sterling 1986). For example, in boll weevil mortality studies, Fillman and Sterling (1983) were able to repeatedly identify over 90% of the causes of individual weevil mortalities to the species of natural enemy or to a single environmental factor. When compared with many other published life tables, 90% is very high. For example, in most published life tables of insects, there is a category called "missing" or "winter mortality" which often accounts for over 25% of the total generation mortality. The durable evidence method is especially applicable to gall insects, boring insects, and insects that feed throughout their immature stages inside fruit, stems, or buds. When these insects die, the evidence of the cause of death may remain on the cadaver or in the feeding tunnel or cell. Prey cadavers in spider webs provide an example of excellent durable evidence.

The use of durable evidence is particularly appropriate for evaluating naticid gastropod predators which mark their molluscan prey with a borehole. Thus a readily fossilized morphological signature of the predation event is available, providing evidence of the success or failure of predation, a measure of the size of the predator, and a simultaneous measure of relevant characteristics of the prey for impact and evolutionary studies (DeAngelis et al. 1985). Similar evidence is probably available for fossilized remains of beetles and other hard-bodied insects.

INACTION LEVELS

As the evidence accumulates concerning the fauna of natural enemies, the next step (Table 2) may be to determine the numbers of the key entomophages needed to maintain the pests at endemic densities below the action (treatment) level (Fillman and Sterling 1985, Sterling 1987). An example of dynamic inaction levels has been provided by studies on the natural mortality agents of the boll weevil (Figure 3).
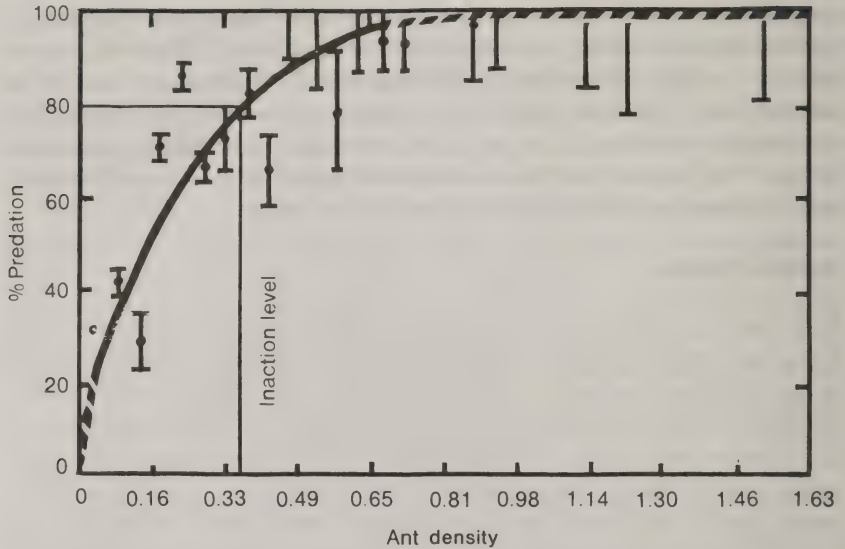
Figure 3. Inaction levels for the red imported fire ant for control of the boll weevil.

In this case, red imported fire ants were the only natural enemy providing evidence of irreplaceable mortality. When ants were removed from the ecosystem, boll weevil numbers increased rapidly (Figure 4).

ESTIMATING ABUNDANCE OF NATURAL ENEMIES

It is a waste of time to attempt to estimate abundance if the species identification of natural enemies is uncertain. Whether the objective of sampling is for research or for pest management, positive identifications are essential. Misidentifications may result in erroneous decisions to spray a "pest" that is really a natural enemy of pests. Thus, one of the first steps (Table 2) in estimating abundance is to learn to accurately identify the natural enemies and the pests.

The publication of manuals containing identification keys and color photographs (Bohmfalk et al. 1983, Rude and Clark 1984) is one way to provide the information needed by samplers. Another way likely to become useful is to present some of this same information on high-resolution color monitors of microcomputers. Laser videodisks containing color photographs of pests and their natural enemies may soon be available to scientists, extension personnel, and farmers (Sterling, unpublished data). Through the use of computers, identification systems with different levels of complexity, depending on the expertise of the user, will be available. Such a system is currently being developed at Texas A&M
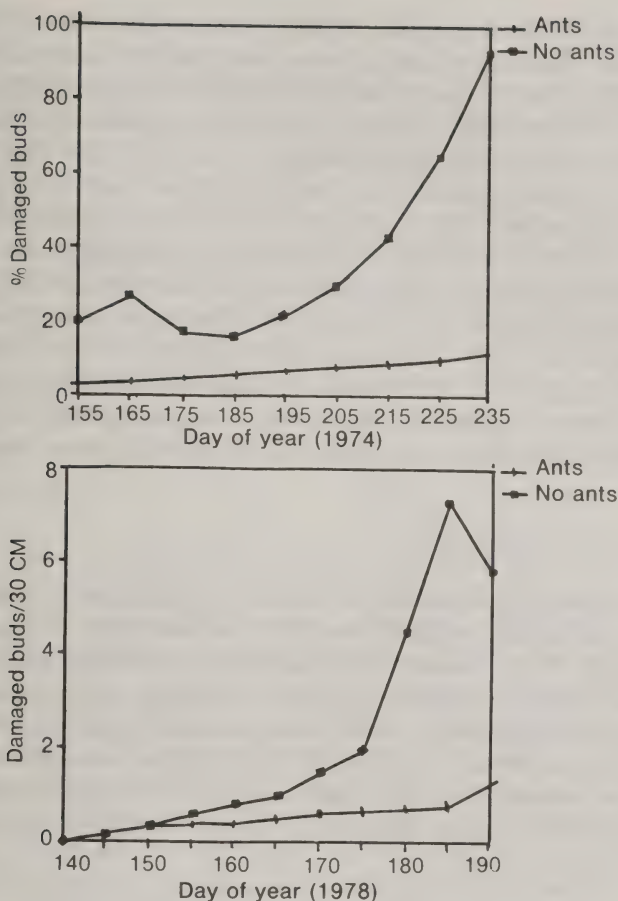
Figure 4. Impact of red imported fire ants on boll weevil abundance based on ant exclusion experiments.

University and a prototype videodisk containing 478 color photos has been produced.

Our intent is to build our second laser videodisk on the compact disk format, complete with insect-plant models, which will be inexpensively available to anyone with a color microcomputer and a compact disk player. We envision farmers (or their consultants) taking samples of pests, natural enemies, plant indices, etc., and entering this information into their portable microcomputers carried in their field vehicles. If there is doubt about pest or predator identifications, simple diagnostic characteristics such as size, color, hard-soft index, shape, etc., which can be entered into the computer, will search out the three or four species fitting the description. For example, an animal with six legs, brown or grey color, and a hard

body might fit the description of only three or four insects found in a cotton field. The unidentified arthropod can then be visually compared to color photos of likely candidates (see Table 2 for the role of identification of natural enemies in learning how to use natural enemies more efficiently).

The advantage of the microcomputer over a paper manual is that large volumes of photographs and information can be searched rapidly in the field. One compact disk is capable of holding all of the information provided in an encyclopedia. Few farmers or consultants are willing to carry an encyclopedia of information in their field vehicles but they could carry several hundred encyclopedias of information stored on compact disks and which could be held in the glove compartment of their auto. Of course the major advantage of such a system would be that farmers could use the computer models to make crop production decisions in the field and minimize the delay in implementing emergency actions when needed.

RESEARCH SAMPLING

Absolute sampling to provide information on numbers per unit area for models and for life budgets have been devised, such as bag samplers (Byerly et al. 1978). Various techniques have been devised that are coming closer and closer to estimating the true density of arthropods. Since no system is 100% accurate, there is a continual need to calibrate techniques against whichever technique provides the highest estimates of density. Since most techniques tend to underestimate the true density, techniques that provide the greatest numbers are likely to be the closest to the true density.

PEST MANAGEMENT SAMPLING

If the dispersion pattern of pests and their natural enemies has been evaluated and the fit to some mathematical distribution is known, then it is usually possible to develop sequential sampling plans for use either in making pest management decisions (Sterling and Frisbie 1981) or for estimating population density. Sequential sampling techniques may reduce sampling time by up to 76% over previous techniques (Rothrock and Sterling 1982). By adding presence-absence sampling methods to sequential sampling, even more time can be saved.

Interest has been expressed recently in the use of Taylor's power law ($s^2 = aX^2$) to increase the biological realism of sequential sampling plans (Wilson 1985, Wilson and Room 1983). Taylor's law can also be used without knowing the underlying dispersion pattern (Ruesink 1980) to calculate sample sizes and confidence intervals needed for a given level of reliability.

RESTORATION ECOLOGY

One question frequently posed concerning the utilization of natural ene-mies is as follows: What methods can be used to restore natural enemies after they have been decimated with insecticides? There may be no quick and easy solution to this question. Time is required for the chemicals to lose their effectiveness and for natural enemies to recolonize. Highly vagile predators and parasites may reach pretreatment densities within 2 weeks following an insecticidal application. On the other hand, total recovery of all natural enemies may require 2 or more years (DeBach 1974). Rotation from crops using extensive amounts of chemical insecticides to crops that can be grown without insecticides should permit restoration of natural enemy effectiveness.

CONCLUSION

Since native natural enemies function quite well without man's interven-tion, relatively little attention is paid to their activities. They often receive little credit for suppressing pest species abundance. Wild native natural enemies have no political or economic constituency; there are no lobbyists in Washington DC or Austin TX, championing the importance of wild beneficial arthropods. There are no company salesmen from some natural enemy company (with the exception of those selling natural enemies for inundative releases) extolling the virtues of natural enemies. Farmers are the only group that benefits substantially from the activities of native natural enemies. Many cotton farmers in Texas realize the benefits they derive from these natural enemies. Others are equally sure that these agents of pest mortality cannot be trusted to do the job.

But it is very likely that without the impact of natural enemies on the pest arthropods, cotton could not be grown profitably anywhere in the world. Why? Because if natural enemies were not having a major impact on pests, and total dependence was placed on chemicals, resistance would build so rapidly that new families of chemicals could not be developed fast enough to solve pest problems. In a short time, pest control would be impossible with insecticides and farmer bankruptcy would be even more common.

Of course the presence of natural enemies is no guarantee that eco-nomic losses will not sometimes result from the actions of pests. Only certain species of natural enemies at certain densities are capable of pre-venting losses to pests. Thus, it is essential to sample for both the pests and their natural enemies to determine the risk of relying exclusively on natural control. If pests are abundant and natural enemies are scarce, then it makes

sense to protect the crop by other means. However, if pests are few and natural enemies are abundant, investments in interventionist tactics (e.g. chemical control or inundative releases of entomophages) may be counterproductive.

The ultimate object of these exercises is prediction. If we can predict the impact of natural mortality of pests, then reliable decisions will minimize risks and maximize benefits. Through the understanding of the mechanisms of natural control we will be able to increase the accuracy of predictions.

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Estimating the Abundance and Impact of Pathogens on *Heliothis* (Lep.: Noctuidae) Populations

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ABSTRACT

Both physical methods and bioassay can be used to estimate the abundance of pathogens of *Heliothis* spp. in the environment. Estimates by physical methods do not necessarily reflect the biological activity of the pathogens. Therefore, associated estimates of pathogen activity should be made by bioassay.

Pathogen abundance, distribution, and survival, and larval feeding rates and behavior normally determine the rate of pathogen acquisition by *Heliothis*. From a knowledge of these parameters and the dosage-mortality responses of the larvae present, the initial mortality due to pathogens applied as microbial insecticides may be predicted. In trials involving microbial insecticides, changes in disease incidence and *Heliothis* population density and age structure at several dose rates should be correlated with crop damage or yield, where possible.

Estimation of the abundance and impact of pathogens on *Heliothis* spp. populations is required to determine both the natural suppression of *Heliothis* by pathogens and the responses of *Heliothis* populations treated with microbial insecticides. Such estimation is difficult because the natural density of pathogens is commonly very low and the distribution uneven (Young 1975). Physical methods, such as microscopy and serology, are relatively rapid, but they do not necessarily indicate the biological activity of the pathogens present. Consequently, estimates of pathogen abundance by physical methods should be calibrated by bioassay for associated pathogen activity (Young 1975).

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ESTIMATING THE ABUNDANCE OF PATHOGENS IN
THE EXTERNAL ENVIRONMENT

Density, Distribution and Survival

Heliothis pathogens in the external environment are normally located in topsoil and on host plants. The soil constitutes an important source and site of accumulation of pathogens. The size and optical properties of pathogens would normally prevent their direct microscopic examination in soil and on plant surfaces. Consequently, methods need to be developed for quantitatively extracting and concentrating pathogens for study.

In soil, pathogens tend to accumulate in the top few centimeters of the soil profile and be retained on clay particles (Evans 1982; Ignoffo et al. 1977). The efficiency of extraction will depend on the clay content of the soil, and would need to be determined for the particular soil sampled. Sampling involves cores of topsoil taken at a number of sites, which may be mixed and subsampled. A method for quantitatively extracting nuclear polyhedrosis virus (NPV) from soil by sonication and sedimentation was detailed by Evans (1982). Following extraction, the NPV is concentrated by centrifugation.

The activity of NPV residues in soil may be measured directly by bioassay, using dilutions of the fine soil fraction in water spread uniformly on the surface of artificial diet (Roome and Daoust 1976). Sprenkel and Brooks (1977) detected overwintering *Nomuraea rileyi* (Farlow) Samson by dusting soil-borne conidia onto the surface of test larvae. In view of the abundant microflora in soil, care would be needed to exclude nonspecific mortality.

On plant surfaces, pathogens can be observed directly by scanning electron microscopy, but the extremely small area of the field would make this method applicable only to concentrated pathogen deposits. NPV must be removed for light microscope examination and this can be achieved using adhesive tape (Davidson and Pinnock 1973; Elleman et al. 1980). Removing the pathogen by washing can be done semi-quantitatively, but this gives less indication of the distribution of the pathogen. It does, however, give a lower detection threshold, by allowing larger samples of plant structures to be used, together with final concentration of the pathogen.

Pathogens applied in sprays can be measured indirectly on plant surfaces or on cards attached to plants by means of tracer dyes, which can be measured colorimetrically after washing off using a solvent (Cunningham 1982). Alternatively, pathogens can be collected on millipore filter membranes for microscopic counts (Morris 1973). Detection and quantification of pathogens can be achieved by direct staining or by immunofluores-

cence (Davidson and Pinnock 1973; Cooper 1979). The initial abundance of *Bacillus thuringiensis* on foliage can be determined by viable spore counts, but, subsequently, allowance has to be made for the fact that spore viability declines at a greater rate than the activity of the endotoxin (Pinnock 1982). Teakle and Stocks (unpublished data) used radioactive (^{125}I-labeled) nuclear polyhedra to trace and measure the NPV released from NPV-killed *Heliothis* larvae on sorghum. The radioactive polyhedra were injected into the cadavers and the radioactivity was measured at different distances from the cadavers. The relative radioactivity in samples over that injected gives an estimate of the proportion of the total virus activity present. The total activity of virus was determined in cadavers of similar size by bioassay. A disadvantage of this procedure is that, because ^{125}I is a γ-emitter, safety considerations preclude these tests from being done under field conditions.

The activity of pathogens on plant surfaces can be estimated by bioassay, usually using leaf disk samples fed to standard larvae under defined conditions, or using washings from contaminated foliage layered onto or incorporated into artificial diet (Beegle et al. 1981). Frequently, a single mortality estimate is made by exposing a number (>60) of test larvae to contaminated samples. Such estimates are subject to considerable imprecision, because of clumping of pathogens, the quantal (all or nothing) response of the test larvae to pathogens, as well as the considerable variation in tolerance of larvae to pathogens, as evidenced by the typically low slopes of the dosage-mortality responses (Burges and Thomson 1971).

Before making comparisons of these estimates it is important that the mortality be converted to pathogen dose (= activity) by reference to the dosage-mortality response. This is determined by standard bioassay, ideally performed under the same conditions. There are numerous examples in the literature of mortality levels being equated with pathogen activity. However, the relationship is not linear, but sigmoid. The dosage-mortality response becomes linear only when the percent mortality is converted to probits and regressed on the logarithm of the pathogen dose. A recorded mortality level of 100% is not quantitative with respect to pathogen dose (= activity), because it is not known if the dose present is the minimum required to achieve 100% mortality, or in excess of this (Payne 1982; Richards and Payne 1982).

Pathogen activity will tend to decline by inactivation rather than by mechanical removal (Payne 1982). Assuming no addition to the pathogen present, a knowledge of the initial activity and the rate of inactivation (mainly caused by UV irradiation in sunlight) should enable the estimation of the activity at a particular time. Pathogen survival can usually be quantified in terms of its half-life ($t_{1/2}$), determined by bioassay after defined periods.
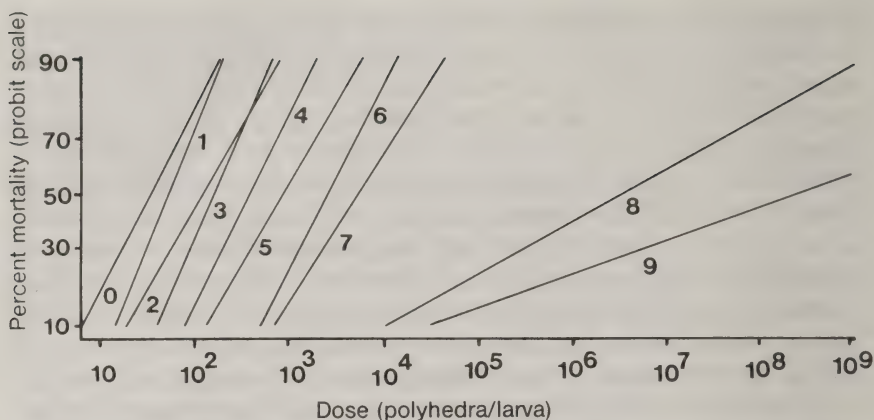
Figure 1. Dosage-mortality responses of *Heliothis armigera,* aged 0 to 9 days, to a commercial nuclear polyhedrosis virus. (Source: Teakle et al. 1985a.)

Dosage-Mortality Response

The dosage-mortality response depends on the type of pathogen (Whitlock 1977; Ignoffo et al. 1983a), the pathogen isolate (Shapiro and Ignoffo 1970), the species of *Heliothis* (Ignoffo et al. 1983b), and the age of the larvae (Allen and Ignoffo 1969; Teakle et al. 1985a). The slope of the dosage-mortality response usually falls between 1.0 and 2.0. The slope of the combined responses of *Heliothis armigera* (Hubner) of ages 0 to 7 days to an NPV was 1.69 (Teakle et al. 1985a). The slopes for older larvae were considerably lower, and LD_{50} values much higher (Figure 1), presumably allowing the survival of a proportion of these larvae during an NPV epizootic.

Feeding Rate and Behavior

Larvae run the greatest risk of ingesting a lethal dose of a pathogen when they feed openly on laminate or small structures, such as foliage or certain flower parts, where the surface area is large relative to their mass. If the pathogen is uniformly distributed, and if the surface area is directly proportional to the mass, pathogen acquisition will then be directly proportional to the feeding rate. As tolerance to pathogens tends to increase with larval age, the increase in feeding rate (virus acquisition) with larval age tends to offset such tolerance. When the age-related increase in feeding matches the increase in tolerance, as with the age-related tolerance of *H. armigera* to an NPV (Teakle et al. 1985a), larvae can display uniform susceptibility over a range of ages. This would not apply where the larva burrows into fruiting bodies and acquires the pathogen only at entry and

exit. The feeding behavior of *Heliothis* on cotton varies with larval age in that first instars feed openly on plant surfaces, whereas later instars tend to feed in concealed locations (Allen et al. 1966). The use of bait formulations may, however, encourage the feeding on contaminated foliage (Bell and Romine 1980).

PREDICTION OF *HELIOTHIS* MORTALITY DUE TO PATHOGENS

If the density, distribution, and survival of a pathogen and the dosage-mortality responses and feeding rates of larvae are known, the mortality of applied pathogens may be predicted (Pinnock and Brand 1981; Payne 1982). Such estimates are desirable to ensure a desired level of kill, or to allow a minimum required dose to be used.

The simplest system involves *Heliothis* larvae feeding on pathogen-treated foliage or flowers, before secondary spread has occurred, or, as with *B. thuringiensis*, where secondary spread does not occur. Cooper (1984) developed a model for such a system, for predicting the mortality of *Heliothis punctigera* Wallengren on lucerne (= alfalfa) treated with a *B. thuringiensis* formulation. The prediction was based on estimates of the initial deposit of *B. thuringiensis* spores on the foliage, the rate of inactivation, and data on the feeding rate of larvae.

Mortality can also be predicted in a particular field situation where all the larvae present essentially have an equal probability of becoming infected by an applied pathogen. Despite the presence of mixed instars, it is then valid to empirically determine a dose-mortality response in the field. This applies to *Heliothis* treated with NPV on sorghum at 100% anthesis. These larvae tend to be young and relatively uniform owing to synchrony of larval development with sorghum head development. Within the range of larval ages present, age-related tolerance is very nearly counteracted by feeding (NPV-acquisition) rate so that susceptibility is independent of larval age (Teakle et al. 1985b).

ESTIMATION OF DISEASE INCIDENCE IN *HELIOTHIS* POPULATIONS

Disease is usually monitored in the larval stage of *Heliothis*, because disease is usually acquired by ingestion of pathogens. In addition, major pathogens, such as NPV, display a high level of specificity for the larval stage. A further reason for studying the disease in larvae is that, besides being the most vulnerable stage, larvae are also directly involved in crop damage. However, mortality in stages other than larvae should not be

disregarded. The fungus *Beauveria bassiana* (Balsamo) Vuillemin causes appreciable mortality in pupae as well as larvae of *Heliothis* (Wilson 1983).

Field estimates of disease incidence tend to grossly underestimate the true incidence. This is because external signs in larvae tend to be relatively inconspicuous or transitory, and, following death, the cadavers often disintegrate or dry out and may be rapidly removed by wind, water, or scavengers. Therefore, laboratory examination is necessary.

Sampling

Systematic sampling of the population is required for accuracy. Generally, sampling methods applicable to parasites and predators are suitable for pathogens, but intuitive, nonstatistical forms of sequential sampling may be used in circumstances where very high or low insect numbers are encountered (Carner 1980). Weekly sampling is usually adequate for long-term monitoring of disease, but more frequent sampling should be made when disease is noted in heavy populations. The transition of disease from the enzootic to epizootic phase can be very brief, and such events may otherwise be missed. In practice, manpower constraints tend to limit sample size and frequency, because of the time involved in handling and examining insects for disease.

Samples of insects from field populations are transferred directly into individual containers in the field, or are transported on specified plant samples to the laboratory. The sampling method should avoid disturbing dead insects or foliage, in order to minimize cross-contamination. The method should also avoid bias to infected insects. For example, the sweep-net method tends to preferentially sample larvae which migrate to the top of the plant prior to death (Newman and Carner 1975). Other potential sources of bias have been listed by Carner (1980). Ideally, when live insects are not held individually, they are cooled to approximately the developmental zero (*ca* 12° C) to immobilize and prevent damage or cannibalism in transit.

Disease Detection

The sampled insects may be examined in two ways, either immediately or after freezing, or after incubation to allow full disease development. The use of both approaches on portions of the same sample may avoid the disadvantages of each (Wigley 1980).

Immediate examination avoids the risk of cross-infection during sampling or subsequent handling, and allows decisions based on pathogens present to be made early (e.g. frequency of follow-up sampling). It is less sensitive than the incubation method, because diagnosis relies on micros-

copic or serological detection of pathogens, and this method may not reveal the subsequent course of the infection.

Incubation of insects to full disease development is simpler and more sensitive and applicable to a wider range of pathogens. Gross pathological symptoms can be employed in making the diagnosis. The rearing conditions should match as far as possible those naturally encountered by the insect to avoid inadvertent suppression of disease development. However, artificial diets are usually used, to minimize handling and the risk of cross-infection or introduction of pathogens on natural plant material. Larvae are transferred to fresh diet after the initial gut contents have been voided, in order to prevent invasion by facultative pathogens or opportunists from the faeces. In order to exclude practically all infections which may have resulted from contamination after sampling, mortality should be recorded immediately after the minimum incubation period for the disease. Contaminants in dead larvae may sometimes be excluded by passaging diseased material through laboratory-reared insects.

Diagnosis

The recognition of disease is usually achieved, or confirmed, by microscopic examination or specific serological tests, such as immunodiffusion (Teakle 1973) or ELISA (Kelly et al. 1978). Guides to the identification of pathogens are by Weiser and Briggs (1971) and Poinar and Thomas (1978).

Associated levels of parasitism should also be recorded, as there is evidence that prior parasitism by *Microplitis* sp. effectively prevents NPV-infection in *H. armigera*. Consequently, in determining the infection rate in the larval population after spraying with NPV, it would be necessary to deduct from the total the number of larvae overtly parasitized (Teakle et al. 1985b).

ESTIMATING THE OVERALL IMPACT OF PATHOGENS ON *HELIOTHIS* POPULATIONS

The selective mortality due to pathogens cannot be simply equated with the non-specific mortality resulting from the use of broad-spectrum chemical insecticides. The retention of beneficials may increase the overall impact on the *Heliothis* population. This can, however, create problems in assessing the net impact of a pathogen on the *Heliothis* population. For example, the retained natural mortality may overwhelm the effects of a pathogen applied as an insecticide (e.g. Teakle et al. 1983), and, for experimental studies, it may be necessary to remove such interference before pathogen treatments are applied (Falcon 1975). A modified

Abbott's formula (Cunningham 1982) can then be used to establish the percent population reduction due to the treatment:

$$
\begin{array}{l}\text{Percent population} \\ \text{reduction due to} \\ \text{treatment}\end{array} = \left[1 - \left(\frac{\begin{array}{l}\text{postspray density} \\ \text{in treatment}\end{array}}{\begin{array}{l}\text{prespray density} \\ \text{in treatment}\end{array}} \times \frac{\begin{array}{l}\text{prespray density} \\ \text{in control}\end{array}}{\begin{array}{l}\text{postspray density} \\ \text{in control}\end{array}} \right) \right] \times 100.
$$

The impact of a pathogen preparation on *Heliothis* is frequently determined indirectly in terms of a reduction in crop damage or increase in yield. The crop protection assessment represents the totality of the insect control and its interaction with the crop. This is frequently done in the context of the evaluation of a microbial insecticide, where *Heliothis* constitutes a key pest. A rate-yield response should always be determined by comparisons of treatments at several application rates and no treatment. To allow comparison with results of other trials, these assessments should be accompanied by estimates of the activity of the pathogen preparation before application and on the crop (Pinnock 1975), and the density and age-structure of the larvae treated.

Subsequently, the disease incidence in the treated populations should be determined, in order to establish a causal relationship between the treatments and the measured effects. Frequently, these details are sketchy or absent in published reports. The age-structure of the population after treatment may indicate the age-component of the population at most risk, and the prolonged absence of final instars may indicate the effective destruction of a larval population for a certain area or duration. Where no differences are recorded between treated and untreated populations, owing to interference from other natural enemies, disease level assessments in sampled larvae may establish the level of control which might have been otherwise achieved.

Attention is naturally focussed on those diseases where host death always follows overt infection, such as those caused by NPV and *N. rileyi*. However the effects of debilitative and persistent pathogens, such as microsporidia and cytoplasmic polyhedrosis virus, should not be overlooked. The activities of these may extend the vulnerable larval stage, and reduce the total number of host generations per season. Comparisons of the reproductive performance of healthy and diseased insects are desirable. However, these may fail to give differences which are statistically significant, because of the uncertain reproductive performance of even healthy, laboratory-adapted *Heliothis*. Parameters such as rates of larval development, pupal weights, and adult longevity, may also provide quantitative estimates of the disease impact of these less virulent pathogens.

Acknowledgment

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Modeling the Impact of Natural Enemies on *Heliothis* spp. [Lep.: Noctuidae] Populations

Keith R. Hopper and *Fred Whitford**

ABSTRACT

We review here explicit mathematical models for predicting the impact of natural enemies on *Heliothis* spp. populations. Potential uses for these models are (1) predicting the impact of natural enemy introduction, (2) predicting the impact of natural enemy augmentation, and (3) deciding whether natural enemy density is sufficient to control *Heliothis* without applying chemical insecticides or augmenting entomophages. General models for predator-prey and host-parasitoid interactions include—for analytical tractability—simplifying assumptions that reduce the usefulness of such models in predicting natural enemy impact on *Heliothis*. Several published models deal specifically with *Heliothis*-entomophage population dynamics or have *Heliothis*-entomophage submodels. These models are often as simple as more general models, but simplicity does not necessarily prevent models from being useful. More serious problems with the natural enemy submodels of *Heliothis*-specific models are that few incorporate field-relevant estimates for parameters and few have been field-tested. The chief obstacles to improved models are lack of knowledge concerning crucial processes (particularly mortality, dispersal, and search rate) and lack of data sets for field tests of models. A division of approaches might lead to better prediction of natural enemy impact on *Heliothis*: models for small areas (e.g., < 1000 ha) and intra-generation dynamics to predict impact of natural enemies on the current *Heliothis* egg and larval populations and models for large areas (e.g.. >100,000 ha) and several *Heliothis* generations to predict impact of natural enemy introductions and augmentations.

INTRODUCTION

Models are simply hypotheses about system structure from which predictions about system state can be deduced. Models of natural enemy impact on pests, either implicit (key processes assumed, but not stated) or explicit

(equations and assumptions stated), underlie every biological control program. In classical biological control (controlling an exotic pest by introducing natural enemies from the pest's homeland), one assumes natural enemies limit a pest in its homeland. Various criteria for selecting natural enemies for introduction have been suggested, and these criteria arise from implicit or explicit models of pest-enemy dynamics (Huffaker et al. 1976; Murdoch et al. 1985). Extrapolation of data on natural enemy impact to conditions different from those where the data were collected requires that change in conditions be unimportant. Thus such extrapolation requires an implicit model of which changes in conditions are important. Others at this workshop will touch on some of these implicit models. This review is restricted to explicit, mathematical models for predicting the impact of predators and parasitoids on populations of species in the genus *Heliothis* (*H. armigera*, *H. punctigera*, *H. virescens*, and *H. zea*) and on the damage that *Heliothis* populations cause.

Modeling is not an end in itself. Potential uses for the models discussed here are (1) predicting the impact of introductions, (2) predicting the impact of augmentation, and (3) deciding whether natural enemy density is sufficient to control *Heliothis* without applying chemical insecticides or augmenting entomophages. First, we discuss published models of herbivore-entomophage population dynamics, both general models and *Heliothis*-specific models, and their potential for predicting the impact of natural enemies on *Heliothis*. Next, we discuss the data available to support such models. Finally, we suggest some approaches to modeling natural enemy impact on *Heliothis*.

GENERAL MODELS

A variety of general models for predator-prey and host-parasitoid interactions have been developed (for reviews, see Royama 1971; Murdoch and Oaten 1975, Hassell 1978, and Hassell and Waage 1984). Because these models have been used for drawing general conclusions and especially conclusions about system stability, simplifying assumptions which allow analytical solution have been made: (1) generations are either discrete and synchronized or births and deaths are continuous; (2) little or no spatial component; (3) little or no age structure; (4) few species; (5) no abiotic factors; and (6) deterministic dynamics. However, as Murdoch et al. (1984, 1985) have suggested, stability of parasitoid-host and predator-prey dynamics may have little to do with the success of biological control, and the assumption of spatial homogeneity may be very misleading. *Heliothis*-entomophage systems meet few, if any, of the above assumptions. Generations are not discrete and synchronized; nor are births and deaths continu-

ous. Furthermore, spatial distribution, age structure, abiotic factors, and stochasticity are important. Thus, these models would not appear to apply well to *Heliothis*-enemy dynamics, and they have not been applied to this system. On the other hand, models are abstractions: they need only incorporate those processes essential to answer the questions they are designed to address. Models must be designed with explicit performance criteria in mind, and then their performance must be compared to these criteria; i.e., models must be validated. Unfortunately, this has rarely been done for general models of insect host-parasitoid or predator-prey dynamics.

MODELS SPECIFIC TO *HELIOTHIS*

Knipling and McGuire (1968) and Knipling (1971) present population models for egg and larval parasitoids, respectively. In both cases, the goals were (1) to decide whether the natural densities of these parasitoids provided sufficient control without intervention and (2) to predict the impact of augmenting parasitoid densities. In these two models, *Heliothis* population growth varies with generation, although not with *Heliothis* density. Parasitoid search is represented by

$$N/H = 1 - \exp\left[(-0.693/d)\,(P/s)\right],$$

where N is the density of parasitized hosts, H is the density of all hosts, P is parasitoid density, d is the parasitoid density which would parasitize half of the hosts, and s is an index of habitat size. This is essentially the same equation as that suggested by Nicholson and Bailey (1935):

$$N/H = 1 - \exp\left[-aP\right],$$

where a is the area of discovery and is equivalent to $-0.693/N$ when P is measured in units of habitat size (s). However, Knipling and McGuire (1968) emphasized the point that the size of host-plant habitat across which a *Heliothis* population is distributed may greatly affect the success of parasitoids, and habitat size changes rapidly during the season of *Heliothis* population growth. These search equations imply that parasitoid search is random and independent of host density and that parasitoid egg supply and handling time are not limiting. Knipling (1971) and Knipling and McGuire (1968) make many of the assumptions made in the general models discussed above; their models contain no age structure, no abiotic factors, no other hosts or natural enemies, no dispersal, and no spatial heterogeneity. Data were not provided for parameter estimates, and no sensitivity analysis of parameter values was reported, but the chief flaw in these efforts is that the models have not been tested against field data for *Heliothis* and its parasitoids.

Hartstack et al. (1976) and Hartstack and Witz (1983) incorporated

predator and parasitoid submodels in a model of *Heliothis* spp. population dynamics (MOTHZV). The goals for this model were to predict *Heliothis* dynamics and impact on cotton in the field. In this model, *Heliothis* development is temperature-driven, natality is moonlight- and temperature-driven, mortality is density-independent, and the *Heliothis* population is age-structured.

Natural enemy population dynamics are modeled explicitly for *Trichogramma* spp. only; densities of other natural enemies are input. *Trichogramma* development and mortality are temperature-driven. *Trichogramma* spp. are treated as one entity, as are larval parasitoid species, but predators are classed into three types based on search rate and *Heliothis* stages attacked. The search equation used is from Knipling and McGuire (1968). Larval parasitoids do not attack *Heliothis* larvae beyond the fourth instar, and predation on larvae is a negative exponential function of larval age. Predation and parasitism act independently; parasitized larvae are removed from the population. Spatial homogeneity is assumed, and neither *Heliothis* nor its enemies disperse. Data were not presented to support the search and mortality rates used, and sensitivity analyses of parameter values for the predator/parasitoid submodel were not reported.

Although Ables et al. (1983) compared predicted maximum larval densities and observed maximum larval densities during the early season (prior 12 July) in 19 cotton fields in 1973, the natural enemy submodel has not been extensively tested against field data. However, the agricultural extension service in Texas have used the MOTHZV model at several locations by Hartstack and Witz (1983), and Goodenough et al. (1983c) conducted simulation experiments on how several management techniques affect *Heliothis* density and cotton yield.

Goodenough et al. (1983b) and Goodenough and Witz (1985) developed new *Trichogramma* spp. submodels for MOTHZV, with the goal of predicting the impact of augmented *Trichogramma* density on *Heliothis* dynamics. They again used the search equation suggested by Knipling and McGuire (1968), but they added effects of parasitoid age and temperature on fecundity, and they made host suitability depend on host age. They improved the development rate and mortality rate representations, and in particular the effects of temperature on these rates. However, search and mortality rates were from laboratory experiments. Goodenough et al. (1983b) and Goodenough and Witz (1985) point out that dispersal of *Trichogramma* may affect parasitization after augmentative releases, but they did not include dispersal in their models. Sensitivity analyses were not reported, and the complete models were not tested against field data, although the development rate sections were tested.

Brown et al. (1983) incorporated a predator submodel in a submodel of *Heliothis* spp. population dynamics (CIM-HEL) as part of the cotton

insect management model (CIM). Their goal was to predict the effects of insect management strategies for *Anthonomus grandis* Boheman and *Heliothis* spp. on insecticide use and cotton yield. *Heliothis* development and natality are temperature-driven. *Heliothis* mortality is density-independent. Predator dynamics are not modeled: predator densities are input. Parasitoids are not considered. *Heliothis* egg mortality rate from predators in Brown et al. (1983) is a constant times predator density. However, this has since been changed to a Nicholson-Bailey search model (L.G. Brown, personal communication). Larval mortality is the same as egg mortality, except for a multiplier that decreases exponentially with larval age. Predator search does not include the effects of temperature, host plant, predator or prey distribution, predator or prey age structure, or predator species composition. Sensitivity analyses have not been reported for the predator submodel, nor have field tests of the predator submodel been reported. However, CIM has been used by a variety of researchers to explore system behavior and economics of *Heliothis* management.

Room (1979) described a prototype model for management of cotton insect pests, chiefly *Heliothis armigera* and *H. punctigera*. The goal was to reduce insecticide applications—and thus development of insecticide resistance, secondary pest outbreaks, and environmental pollution—while maintaining economic return. Thus, a computer model was designed to make decisions for management of individual fields, based on scouting data about insect densities and crop status. This model, now called SIRATAC, has been revised several times (Hearn et al. 1981, Ives et al. 1984, Hearn and Da Roza 1985). In the original version, *Heliothis* density was predicted only for the next day. Predators consumption (C) was given by:

$$C = S \, (1 - \exp \, (- \, 0.07 \, P),$$

where S is satiation and was calculated by summing the product of predator densities and consumption capacities of predator species for each age class of *Heliothis*, and P is the density of all prey species. This consumption was converted to *Heliothis* mortality by multiplying by the proportion of total prey which was *Heliothis*. In subsequent revisions, prediction of *Heliothis* was extended to 2 days so that sampling frequency could be reduced. Hearn et al. (1981) reported that they were unable to assess impact of individual predators in the field so that they replaced this relatively complex submodel with a step function increase in *Heliothis* mortality when the density of all predator species exceeded 10 individuals/ row-meter. Sensitivity analyses have not been reported for either predator submodel, nor have field tests of the predator submodel been reported. However, a grower-controlled company, SIRATAC Limited, has adopted the SIRATAC model, and the model was used on 27% of the cotton acreage in Australia during the 1984/85 season (Hearn et al. 1985).

MODEL SIMPLICITY

These *Heliothis*-specific models do not include many more variables or relations than general models of prey-predator or host-parasitoid dynamics. The major additions are age structure and temperature-driven development rate for *Heliothis*. However, simplicity is not necessarily a problem. Modelers sometimes incorporate processes in a model because they are known to occur, whether or not they are important in the system modeled. For example, host/prey density is thought to affect natural enemy search rate through increased handling time and satiation (either because of limited gut capacity for predators or limited egg supply for parasitoids). However, several studies have shown that predation rates and parasitization rates are independent of *Heliothis* density over the range of densities that natural enemies are likely to encounter in the field (Hutchinson and Pitre 1983; Hopper and King 1986). Models are abstractions: they should contain only those variables and relations necessary to answer the question at hand.

DATA NEEDS

A more serious problem with the above models is that few incorporate field estimates for crucial parameters and relations. Modelers are not solely to blame for this shortcoming; indeed, these modeling efforts have brought out clearly the gaps in our knowledge of *Heliothis*-entomophage dynamics. Furthermore, much ground work data collection has been done on *Heliothis* natural enemies: many surveys have been done on the phenologies, host-plant associations, and geographical distributions of *Heliothis* natural enemies, and many laboratory studies have been done on behavior, development, fecundity, mortality, and prey consumption of *Heliothis* natural enemies (see Kogan et al. 1978 for a bibliography covering some of this work). Furthermore, important studies have been done on *Heliothis* defenses, impact of parasitization on host behavior, semiochemicals, and interaction of natural enemies with insecticides and host plant resistance.

However, few of the relations and parameters necessary for building models have been measured, and even fewer have been measured in a way relevant to the field. We have reviewed the literature on *H. zea* and *H. virescens* natural enemies to find data that could be used in simple models of natural enemy impact. In Table 1, we summarize studies on ten predator and ten parasitoid species that give data on consumption capacity of predators; impact of parasitization on crop damage; and development, fecundity, mortality, search rate, host/prey preference, and dispersal of

predators and parasitoids. We have included only those studies that could actually provide parameter estimates, and for search rate, mortality, and dispersal, only those studies that provide field-relevant estimates. Thus, we have excluded surveys of temporal or geographic distribution. We have also excluded studies that demonstrate that a variable is important but that do not allow parameter estimation. The influence of other factors (e.g., temperature, host plant, *Heliothis* density) on most of the listed variables have not been tested for most species. Simple models that predict mortality or parasitism from data on densities of *Heliothis* and natural enemies require estimates of search rates. Yet accurate, field-relevant search rates and functional responses have been published for only a few predators and parasitoids of *Heliothis*.

Table 1. *Literature providing data for parameter estimates in modeling the impact of natural enemies on* H. zea *and* H. virescens

Natural enemy species	Variables*	Sources
Archytas		
marmoratus	Fecundity	Gross and Johnson (1985)
	Search	Gross and Young (1984)
	Development, fecundity, mortality	Hughes (1975)
Chrysopa		
carnea	Consumption, preference	Ables et al. (1978)
	Search	Barry et al. (1974)
	Mortality	Bull and House (1978)
	Consumption, search	Butler and May (1971)
	Consumption, preference	Henneberry and Clayton (1985)
	Consumption, search	Lopez et al. (1976)
	Mortality	Pitts and Pieters (1982)
	Search	Ridgway and Jones (1986)
Coleomagilla		
maculata	Search	Bryson and Schuster (1975)
	Consumption	Lopez et al. (1976)
	Search	McDaniel and Sterling (1979)
Cotesia		
marginiventris	Development	Boling and Pitre (1970)
	Development	Hamm et al. (1983)
	Mortality	Lingren et al. (1972)
Cardiochiles		
nigriceps	Development	Butler et al. (1983)
	Preference	Hays and Vinson (1971)
	Development, preference	Lewis and Brazzel (1966)
	Development	Lewis and Vinson (1968)
	Preference	Lewis and Vinson (1971)

Natural enemy species	Variables*	Sources
	Search	Lewis et al. (1972)
	Development	Vinson et al. (1973)
Campoletis perdistinctus	Preference	Lingren and Noble (1972)
	Mortality	Lingren et al. (1972)
	Preference	Lingren et al. (1970)
	Development, fecundity, search	Noble and Graham (1966)
Campoletis sonorensis	Mortality, search	Lingren and Lukefahr (1977)
	Preference	Schmidt (1974)
Eucelatoria armigera	Development	Bryan et al. (1970)
	Development	Jackson et al. (1969)
	Development, fecundity	Ziser and Nettles (1978)
	Development	Ziser et al. (1977)
Geocoris punctipes	Consumption, preference	Ables et al. (1978)
	Search	Ali and Watson (1982)
	Search	Barry et al. (1974)
	Consumption	Brown and Goyer (1984)
	Development	Butler (1966)
	Consumption, preference	Chiravathanapong and Pitre (1980)
	Development	Cohen and Debolt (1983)
	Consumption, preference	Ewing and Ivy (1943)
	Search	Hutchison and Pitre (1983)
	Consumption, development, preference	Lawrence and Watson (1979)
	Consumption, search	Lingren et al. (1968a)
	Mortality	Lingren et al. (1968b)
	Consumption	Lopez et al. (1976)
	Search	McDaniel and Sterling (1979)
	Search	McDaniel et al. (1981)
	Consumption	Thead et al. (1985)
Hippodamia convergens	Consumption, preference	Ables et al. (1978)
	Mortality	Bull and House (1978)
	Consumption, preference	Ewing and Ivy (1943)
	Consumption, preference	Henneberry and Clayton (1985)
	Consumption, search	Lingren et al. (1968a)
	Mortality	Lingren et al. (1968b)
	Search	McDaniel and Sterling (1979)
	Mortality	Pitts and Pieters (1982)
Microplitis croceipes	Development	Bryan et al. (1969)

Natural enemy species	Variables*	Sources
	Damage, development	Hopper and King (1984a)
	Development, preference, search	Hopper and King (1984b)
	Search	Hopper and King (1986)
	Development	Hamm et al. (1983)
	Development	Jones and Lewis (1971)
	Development, preference	Lewis (1970)
	Development	Lewis and Burton (1970)
	Fecundity, preference	Lewis and Snow (1971)
	Preference	Mueller (1983)
	Development	Powell and Lambert (1984)
	Mortality	Powell and Scott (1985)
Nabis alternatus	Consumption, search	Lingren et al. (1968a)
	Mortality	Lingren et al. (1968b)
Nabis americoferus	Mortality	Stoltz and Stern (1979)
	Development	Braman et al. (1984)
Orius insidiosus	Consumption, preference	Ables et al. (1978)
	Consumption	Brown and Goyer (1984)
	Consumption, preference	Ewing and Ivy (1943)
	Development	Isenhour and Yeargan (1981)
	Consumption, search	Lingren et al. (1968a)
	Mortality	Lingren et al. (1968b)
	Search	McDaniel and Sterling (1979)
	Search	McDaniel and Sterling (1982)
	Search	McDaniel et al. (1981)
Oxyopes salticus	Consumption, search	Lingren et al. (1968a)
	Search	McDaniel and Sterling (1979)
	Search	McDaniel et al. (1981)
	Development, fecundity	Whitcomb and Eason (1967)
Reduviolus roseipennis	Search	Donahoe and Pitre (1977)
	Consumption, preference	Nadgauda and Pitre (1978)
Solenopsis invicta	Consumption	Agnew and Sterling (1982)
	Search	McDaniel and Sterling (1979)
	Search	McDaniel and Sterling (1982)
Trichogramma exiguum	Development	Harrison et al. (1985)
	Search	Thorpe and Dively (1985)
Trichogramma minutum	Dispersal, preference, search	Fye and Larsen (1969)
	Search	Thorpe and Dively (1985)

Natural enemy species	Variables*	Sources
Trichogramma pretiosum	Search	Ables et al. (1980)
	Search	Ashley et al. (1974)
	Mortality	Bull and House (1983)
	Development	Goodenough et al. (1983a)
	Search	Gross et al. (1984)
	Development	Harrison et al. (1985)
	Search	Lewis et al. (1976)
	Mortality	Lopez and Morrison (1980)
	Search	Morrison and Lewis (1981)
	Fecundity	Stinner et al. (1974a)
	Dispersal, mortality, search	Stinner et al. (1974b)
	Search	Thorpe and Dively (1985)

*Consumption = number of prey consumed per time; damage = effect of parasitization on damage done to crop; development = time taken for life stages; dispersal = distance dispersed per time; fecundity = number and sex ratio of progeny produced per time; mortality = number dying per time; preference = frequency of prey/hosts attacked vs frequency available; search = habitat area searched per time.

MODEL VALIDATION

The most serious problem with the models reviewed here is that they have not been tested in the field, and, in most cases, performance criteria have not been suggested for such tests. However, MOTHZV, CIM, and SIRATAC were not designed primarily for predicting natural enemy impact, so that field tests of the natural enemy submodels may be asking too much. In any case, the above list of parameters and relations necessary for intergeneration models may be wrong, and much simpler models may suffice, but we will never know whether our models suffice if we do not test them in the field.

Possible Approaches

A division of approaches might lead to better prediction of natural enemy impact on *Heliothis*. First, decisions on *Heliothis* management are presently made for individual fields or farms in most areas. Models for a small spatial scale (e.g., an individual field) and short time horizon (e.g., 1 week) could be used to predict impact of natural enemies on the *Heliothis* egg and larval population currently in a field. Such models might only require equations for the impact of *Heliothis* larvae on the crop and for the number of *Heliothis* eggs and larvae attacked by predators and parasitoids. Thus, data would be needed on *Heliothis* feeding and mortality and on

predator/parasitoid search and mortality rates. Although data on these variables are thin, more data are available than are used in current *Heliothis* management. One significant drawback to such models is that they require frequent sampling (e.g., once or twice a week) of densities of both *Heliothis* and natural enemies. Thus cheap, but accurate, sampling methods are needed for practical use of such models. Given the high mobility of *Heliothis* (Hendricks et al. 1973; Haile et al. 1975; Sparks et al. 1975; Snow et al. 1979; Hartstack et al. 1982; Proshold et al. 1983; Daly and Greg 1985), predictions over longer time periods for individual fields, which would allow less frequent sampling, may never be possible.

Intergeneration models are needed for predicting impact of introductions and intergeneration effects of augmentation. These models need not include the impact of *Heliothis* on crops. However, they would include natality, mortality, and dispersal of *Heliothis* and natural enemies, as well as the search rates and host and host-plant preferences of natural enemies. One approach would be to subdivide a region into areas of local dynamics without dispersal and model the dispersal between local areas. Such models need not predict insect densities in individual fields, but they might predict the frequency distribution of densities across fields. We do not have the data to build such models at present; in particular, we know next to nothing about dispersal of *Heliothis* and its natural enemies. Lack of knowledge about insect dispersal is a key gap in the understanding needed for rational pest management.

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The Economics of Biological Control
of *Heliothis*

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ABSTRACT

The economic factors that determine the feasibility of any given biological control technique are discussed. Biological control is not likely to be fully employed on high value crops such as cotton in the United States of America as long as effective insecticides are available. The complexities of the cotton ecosystem, in the midsouth region of the USA, are discussed and an example is presented using simulation modeling to evaluate beneficial arthropods in cotton production systems. The results of simulations run with varying combinations of pests and beneficial populations enable the actual monetary value of predatory arthropods in two regions to be ascertained. Increasing the level of beneficials in the presence of light to medium levels of *Heliothis* resulted in increased yield and reduced insecticide usage.

INTRODUCTION

This paper is divided into two sections. The first section deals with biological control (primarily entomophagous arthropods) in general and the second section discusses a technique for the estimation of the economic value of beneficial arthropods in commercial cotton.

BIOLOGICAL CONTROL

The economic feasibility for any given biological control technique is determined by a range of economic factors (Reichelderfer 1981). Economic feasibility is greatest for tactics that are targeted against consistently

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occurring light or moderately damaging single, major pest species on high-value crops; tactics that are highly efficacious, relatively risk-free, and low-cost; and tactics that compare favorably with available chemical control alternatives. In most modern agricultural production systems, biological control techniques have not been adopted because of multiple pests and a low degree of efficacy, and because chemical alternatives are superior in terms of benefit-cost (B/C) performance. An economic study in Australia (Lee 1981) shows that biological pest control is often not cost-effective. It seems highly unlikely that biological control of *Heliothis* on crops like cotton in much of the USA will ever be accepted in commercial agriculture (as long as chemical insecticides are effective) because of the many pests that attack the crop over the crop season.

However, there may be a place for biological control in some of the underdeveloped and developing countries with traditional peasant agricultural production systems. Consider low value or human consumption crops with no market value in a primitive agricultural production system. Specifically consider chickpea or pigeonpea—two crops that are damaged by *Heliothis* worldwide—for human consumption. Moreover, assume we have a biological control technique that can increase yield 50% at a relatively low per hectare cost, i.e., cost much less than returns where market price exists. Following are four situations where these assumptions are made:

Situation 1—Consider a slash-and-burn agriculture with no markets, no limitation on land, with excess labor, and a need for additional food. In this situation, even with the cost of biological control well below inputted returns, the fact that we have unlimited land, excess labor, and no markets means that the technology will not be utilized; i.e., there is no economic incentive. The need for more food is met simply by expanding acreage. This situation is extremely rare and, in fact, may no longer exist.

Situation 2—Consider the same production/market system but without excess labor. Under such assumptions, the peasant farmer would be "better off" if the technology could be adopted (provided human consumption requirements are not being satisfied).

Situation 3—Consider the same production/market system but with limited land. Again, the peasant farmer would be "better off" if he could employ the technology.

Situation 4—Consider the same production system but with markets for the output and with limited land or labor. This case is fairly common. Typically, many developing countries have limited land, high rates of unemployment (or excessive underemployment), and are net importers of food items. In this situation there will be economic incentive to

augment the technology even if current human consumption require-ments are being satisfied because the additional production can be sold. A market could develop for the technology and the peasant farmer could purchase the technology, could employ it, produce food beyond family requirements, sell the surplus, and buy other needed items, i.e., raise his standard of living.

In situations 2, 3, and 4, the technology is not likely to be augmented through traditional market channels because of the lack of markets and/or because of a lack of understanding of the process by the peasant grower. The backbone of a market economy is knowledge and information. The educational process required to bring peasant farmers up to the necessary level of knowledge would be viewed as excessively expensive by most such countries and would require several years to occur. Fortunately (from a biological pest control standpoint), in most countries experiencing these situations, the economic system is centrally planned. A centrally planned economy can easily augment biological control techniques that would never be readily augmented through a market economy.

An important difference between insect control on a crop like cotton in a developed country such as the USA and pest control on a food crop like pigeonpea in an underdeveloped country is the current technology being utilized or employed to control the pest(s). In the U.S. cotton situation, the current practice is to use chemical insecticides. Their costs have been institu-tionalized into the domestic price of cotton. For biological control to replace chemical control, it must be superior in economic terms; i.e., give improved control at the same cost or equal control at reduced cost. However, in countries where the current insect control practice is "nothing," biological control, to be economically feasible, only needs to have a favorable B/C ratio, i.e., the value of the additional output (yield), either real (based on market price of the output) or inputted, must be greater than its cost.

In conclusion, biological control is not likely to be employed on high-value crops such as cotton in the USA unless chemical control procedures fail. It is more likely to be used on low- or zero-value human consumption crops in developing countries, but the process will likely require some phase of governmental intervention.

ECONOMIC VALUE OF BENEFICIAL ARTHROPODS IN COMMERCIAL COTTON IN THE U.S. MIDSOUTH

The U.S. midsouth (Mississippi Valley) is one of the major cotton-producing regions in the USA, with the largest cotton acreage being in the state of Mississippi. About 80% of the cotton in Mississippi is produced in

the Yazoo-Mississippi Flood Plains (Delta) on alluvial soils. The remaining 20% is grown in the hill section or non-Delta portion of the state, primarily on Loess soils. Cotton is produced in the midsouth by applying modern technology: labor requirements are minimal and capital requirements are quite large. High rates of nitrogen fertilizer are employed. Weeds and insects are controlled by the application of chemical herbicides and insecticides. However, since the late 1960's, when *Heliothis* spp. started to become resistant to available insecticides, IPM (integrated pest management) techniques have been employed to make use of naturally occurring populations of entomophagous arthropods.

The economic value of beneficial arthropods will vary considerably across the 13 states of the U.S. cotton belt. Some variation can be expected within the midsouth. Because the state of Mississippi has two distinct cotton agroecosystems, specific examples in this paper will focus on the cotton grown in the state of Mississippi.

Currently, beneficial arthropods on cotton in the midsouth mean predators and parasites of *Heliothis* spp. However, any effort to approximate the economic value of beneficials requires a detailed understanding of all insects involved (beneficials and pests), as well as a complete understanding of the phenology of the cotton crop.

Key Pests

A key pest is defined as a perennially occurring and persistent pest that dominates control practices. The boll weevil, *Anthonomus grandis* Boheman (Harris 1973), is the key pest of cotton in the midsouth, although this point is argued by some entomologists in the Delta area of Mississippi, where boll weevils survive in relatively low numbers. Currently, the secondary bollworm complex appears to be a more important problem. A historical point of view and an understanding of the ecological upsets caused by pesticides, however, lead one to realize that the boll weevil was the pest that started the "pesticide syndrome" (Drea et al. 1973) in cotton in the midsouth. Thus it is largely responsible for the release of secondary pests and other pesticide-related problems.

Occasional Pests

Plant bugs and fleahoppers
The tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), and the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), are occasional pests that create problems in some areas of the midsouth in some years. The relative importance of these two bugs is not known. Their pest status is also unknown where in-season pesticides for boll weevil control are eliminated over a wide area for a sustained period of time. The known

potential of the plant bugs to cause serious crop damage makes them important. These pests might be elevated to key pest status in a system where they are not being controlled by insecticides applied for boll weevil and bollworm control.

Thrips

Thrips can be categorized as occasional pests of cotton in the midsouth, and their significance to pest management schemes for other cotton pests is not known. Cotton plants often recover from thrips injury with no measurable effect later in the season, but severe thrips injury can reduce stand, retard plant growth, delay crop maturity, and reduce yield (Heimpel 1974). Thus thrips control practices interact with agronomic, disease control, weed control, and harvest practices.

Other occasional pests

Several other pests of cotton are characterized as occasional, because they occur periodically, are not particularly related to control of any other pest, and require insecticide treatments for their control. These are cutworms, aphids, cabbage looper, and armyworms.

Secondary Pests

Two important secondary pests occur on cotton in the midsouth; they have been elevated to pest status or have become more significant because of pesticides applied for key or occasional pests.

The bollworm, *Heliothis zea* (Boddie), and the tobacco budworm, *H. virescens* (F.), are the most important secondary pests of cotton in the midsouth. The larvae of both these insects are difficult to control, especially the mid and late instars—even when the populations are susceptible to the insecticides being used. Increasing resistance to insecticides in these *Heliothis* species, especially the tobacco budworm, has frequently made economic control very difficult. During 1969 and 1972 and again in 1976 and 1977, high-density tobacco budworm infestations occurred late in the season on cotton in the midsouth. Since the introduction of pyrethroid insecticides in 1978, *Heliothis* spp. problems have been relatively minor. Whether this is due to the effectiveness of the new compounds or to unknown naturally occurring regulating factors is not yet known.

RELATIONSHIP OF INSECT PESTS TO COTTON CROP DEVELOPMENT

Certain aspects of the seasonal development of cotton are shown in Figure 1: the stages of development, or events that occur, as a cotton crop
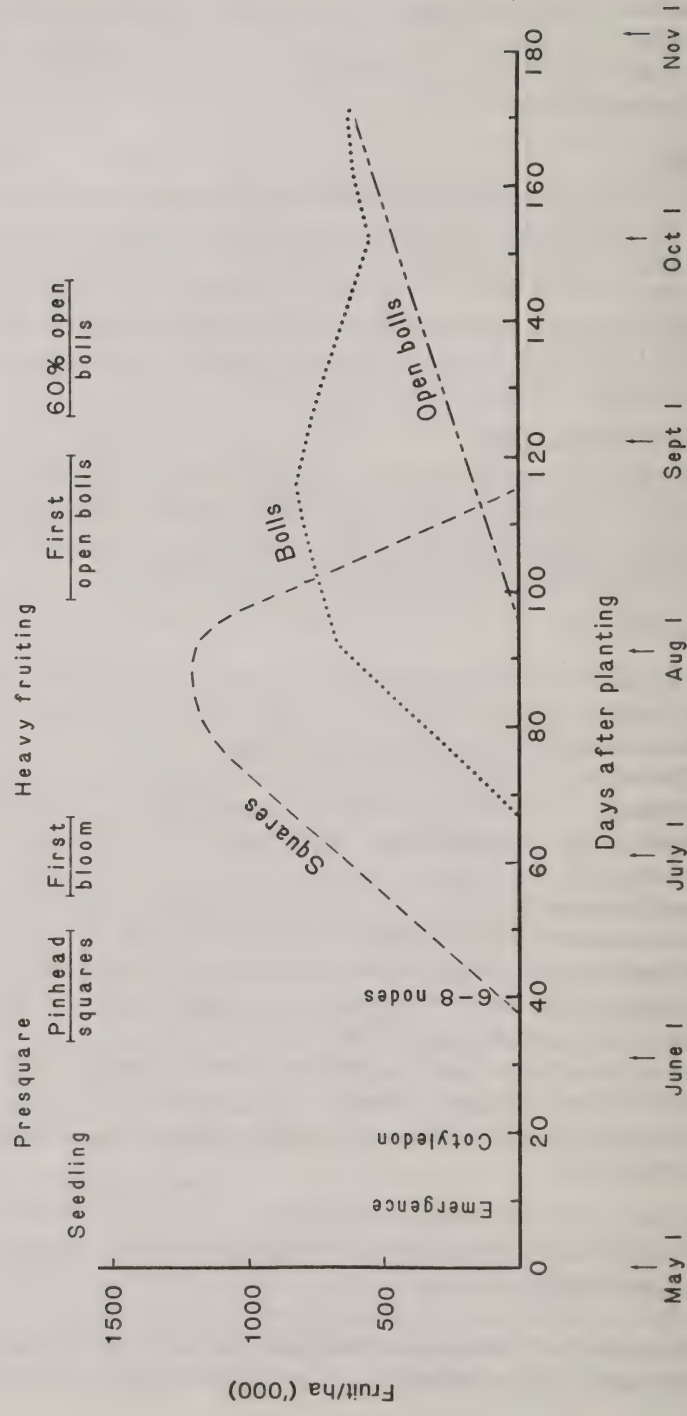
Figure 1. Seasonal development of cotton in the U.S. midsouth.

progresses through the growing season. Also indicated are major insect pests for various periods during the season.

Figure 1 illustrates a crop planted on 1 May. However, planting dates may be as early as 10 April and under adverse conditions extend into late May. The seedlings usually emerge in 5 to 8 days. The seedling stage, cotyledon to two true leaves, will last about 10 days, followed by the presquare stage, which is also about 10 days. In early June the first flower buds (squares) appear. This stage is called the "pinhead square stage" because the fruit on the plants are very young, tiny flower buds. In 20 to 25 days after the first squares appear, the crop will begin blooming. When the first blooms appear, the crop is normally in a state of highly accelerated fruiting, which reaches a peak in late July and early August.

This period of accelerated fruiting in July and August is extremely important. The crop usually will have the best growing conditions during this period, with the fewest external and internal stresses. Bolls set during this period mature faster and produce higher quality lint and seed than those set at other times.

The crop begins to rapidly set bolls in August. These bolls have high demands for carbohydrate which must be produced by photosynthesis; thus a kind of internal stress is created in the plants. At this stage, external stresses, such as prolonged cloud cover or drought, cause shedding of squares, blooms, and young bolls. These natural shedding events will occur even in the absence of insect pests.

As the crop matures in late August and September, the bolls begin opening and a decision to apply a chemical defoliant is based on 60% open bolls (usually between mid-September and mid-October).

Insect pest management in cotton extends from preseason planning through the season and ends with a fall program of controlling diapausing boll weevils. The following discussion relates insect problems to the seasonal development of the cotton crop.

Seedling stage

Thrips are the predominant pest during the 10- to 12-day seedling stage (Figure 2). Occasionally, thrips will damage cotton for a longer period, but this is not common. Aphids and cutworms are occasional pests on seedling cotton and must be controlled when threshold levels are exceeded.

Early season

The early-season stage, i.e., presquare to pinhead square to prebloom stage, is a critical decision period for insect pest management. Plant bugs and fleahoppers moving into cotton during this stage (Figure 2) can delay crop maturity and reduce yield. Insecticidal control late in this stage increases chances of increasing bollworm and tobacco budworm popula-
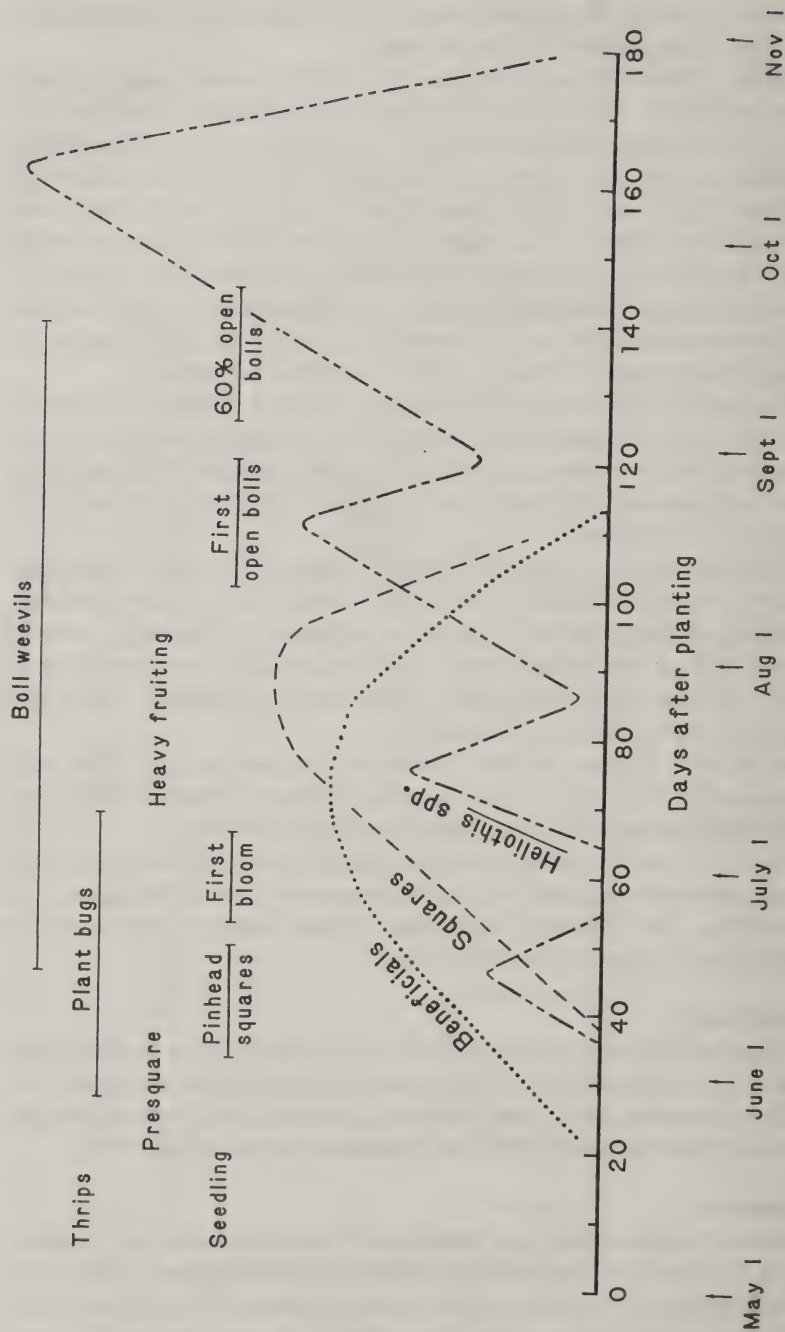
Figure 2. Seasonal chart of cotton insects in the U.S. midsouth.

tions, because their natural enemies are destroyed. Boll weevils, emerged from hibernation, begin laying eggs in young squares during this period. Beneficial arthropods begin building up in the cotton at this time. Spotty infestations of spider mites occasionally develop during early season (and subsequent stages of the crop). For several reasons—fruiting rate and pest and beneficial insect infestation rates—the stage is being set for the remainder of the season.

Midseason

The period from first bloom through heavy fruiting is the critical time for setting the bolls that will mature during the late season. Although midseason losses to insects might occur, this period is, at least theoretically, less likely to need insecticide applications under good insect pest management practices. If early-season plant bugs, fleahoppers, and over-wintered boll weevils are a problem, control should be initiated early enough to allow the recovery of natural enemies for suppression of boll-worms and tobacco budworms if beneficial arthropods are to be of meaningful economic value. Reproduction-diapause control of boll wee-vils the previous fall should alleviate economic infestations of boll weevil during midseason.

Late season

The late-season period from first open bolls to 60% open bolls usually occurs from late August through mid-September to late September. Boll weevil or bollworm and tobacco budworm infestations, or both, reach their highest peaks during this period and insecticides are usually applied to control them.

Fall program

The reproduction-diapause boll weevil control program is designed to kill boll weevils in the fall, before they enter hibernation sites to spend the winter. The minimum requirement is one insecticide application with the defoliant in areas where weevil populations are low and the crop does not produce regrowth after defoliation. In most cases, the maximum fall program would consist of four applications: one between the last in-season treatment and defoliation, one with the defoliant, and two applications at 10- to 14-day intervals after defoliation.

CROP PHENOLOGY AND INTEGRATED PEST MANAGEMENT

Predatory and parasitic arthropods are considered insect regulators within most ecosystems. The conservation of beneficial arthropods is central to most integrated pest management systems in agriculture. The use of bene-ficial arthropods as regulator agents against *Heliothis* within the cotton

agroecosystem is a prime example. Naturally occurring beneficial arthropods (predators and parasites) have long been considered important in regulating the numbers of *Heliothis* (Quaintance and Brues 1905, Fletcher and Thomas 1943, Ewing and Ivy 1943, Wille 1951, Whitcomb and Bell 1964, van den Bosch and Hagen 1966, Ridgway et al. 1967, Lingren et al. 1968, van den Bosch et al. 1969). Therefore, it is not surprising that conservation of beneficial arthropods is a fundamental part of the cotton integrated pest management concept.

The ability of the cotton plant to compensate for damage is widely recognized (Blackwell and Buie 1924, Eaton 1931, Hamner 1941, Dunnam et al. 1943, Harris 1974, Townsend 1974, Bottrell and Adkisson 1977, Brown et al. 1977, Barnes et al. 1979). Tugwell and Waddle (1974) reported that 80 to 95% of fruit (primarily squares) shed by a typical plant was due to climatic conditions, and the rest to insects. This removal of fruit results in a "pruning" effect on the plant. The reduced number of fruit causes a reduced demand for carbohydrate and nitrogen which, in turn, allows the plant to set other fruit or to put more lint in the bolls already set. Thus, the relationship between injury and yield varies with the growth stage of the crop at the time of damage (Harris 1975).

Simply stated, the current recommended integrated pest management system for insect control in cotton in the midsouth is to allow predatory and parasitic arthropods to build up in cotton during the early season, so that they can help to control mid-season *Heliothis* populations. This approach fails in the midsouth when early-season populations of boll weevils and/or plant bugs must be treated with "hard" insecticides during the early season and/or beneficial populations do not reach high enough levels. To avoid this, entomologists were generally agreed that a practical approach would be to control boll weevils by eradication or with fall chemical applications to prevent diapause and overwintering. Also, plant bug thresholds could be kept artificially high to reduce insecticide application in the early season, because of the plant's ability to compensate for early-season damage.

Until recently, the general view of the impact of plant bugs and other early-season insect pests on cotton was that they delayed maturity but did not decrease yield. However, recent work (Parvin 1985, Parvin et al. 1985) has shown this to be a misunderstanding arising from the difference between experimental yield and producer yields. Experimental yields are obtained on a sample basis and in a very short time period—usually less than one-half of one day. Producers harvest over an extended period. The harvest season in the midsouth requires approximately 240 hours. Actually, due to weather and other factors, it takes approximately 30 calendar days to complete the first harvest and about 45 calendar days to complete the second harvest.

Experimental trials where yields are obtained on a rather instantaneous basis can result in yield estimates in which the cotton seems to have compensated for the early damage or delay in maturity. But in commercial cotton, due to the length of the harvest season, a delay of 1 week reduces yield by 7% on an average, while a delay of 2 weeks reduces yield by 16%. These reductions are a function of decreased picker efficiency over the harvesting season and not due to decreased agronomic yield. Improvement in crop maturity will increase harvesting efficiency, commercial yield, and returns, even though agronomic yield is unchanged.

Recent research is beginning to question the concept that fruit formed during the accelerated fruiting period in July and August is more important than the fruit formed during the first few weeks of squaring (primarily in June). This work is summarized in Tables 1 and 2.

Table 2 indicates that by the time the second generation *Heliothis* is over (see Figure 2), 64 to 88% of the crop can, if protected, already be nonsusceptible to *Heliothis* feeding. Consequently, the concept of accepting early-season damage, primarily from boll weevils and/or plant bugs, to conserve beneficial arthropod populations to help control *Heliothis* spp. is currently being reevaluated.

Clearly, the cotton ecosystem in the midsouth is a remarkably complex

Table 1. *Percent of yield, boll set, square shed, and bolls per kg of seed cotton by week of squaring*

Week of squaring	% of yield	% boll set	Bolls/kg seed cotton	% square shed due to	
				Insects	Other stress
1	21	94	192	96	4
2	43	78	216	97	3
3	24	43	271	95	5
4	9	21	355	85	15
5	2	13	322	87	15
6	1	11	308	68	32

Source: Columns 1–4 (Hamner 1951); Columns 5–6 (Mauney & Henneberry 1984).

Table 2. *Dates of squaring and blooming, dates bolls are no longer subject to* Heliothis *spp. feeding, % yield, and % cumulative yield by week of squaring; cotton planted 1 May, U.S. midsouth*

Week	Date of Squaring	Date of blooming	Date bolls are no longer subject to feeding by *Heliothis* spp.	% yield	% cumulative yield
1	7–13 June	30 June–1 July	20–26 July	21	21
2	14–20 June	7–13 July	27 July–2 Aug.	43	64
3	21–27 June	14–20 July	3–9 Aug.	24	88
4	28 June–4 July	21–27 July	10–16 Aug.	9	97

unit. Therefore, a proper economic evaluation of one factor (such as beneficial arthropods) will be difficult. At present, it is impossible to obtain all the necessary knowledge to fully understand the many factors related to beneficial arthropods (and their interactions) which influence the yield and value of cotton in the midsouth.

The typical approach with problems of this type is to abstract from the complex detail of the real world to a simpler hypothetical system that can be analyzed and to assume that the simplifying reductions do not mask important relationships. To minimize the number of simplifying assumptions, simulation models for cotton (Brown et al. 1979), *Heliothis* (Parker et al. 1975), and boll weevils (McClendon et al. 1977, Jones et al. 1975) were interfaced in an overall simulation model with the effect of predators and insecticides included.

SIMULATION OF THE COTTON ECOSYSTEM

At Mississippi State University, Mississippi State (USA) and the USDA (U.S. Department of Agriculture), simulation models have been developed of the cotton crop, *Heliothis*, and boll weevil populations. These models have been interfaced as shown in Figure 3 to study the effects of different insect populations (pest and beneficial) on yield.
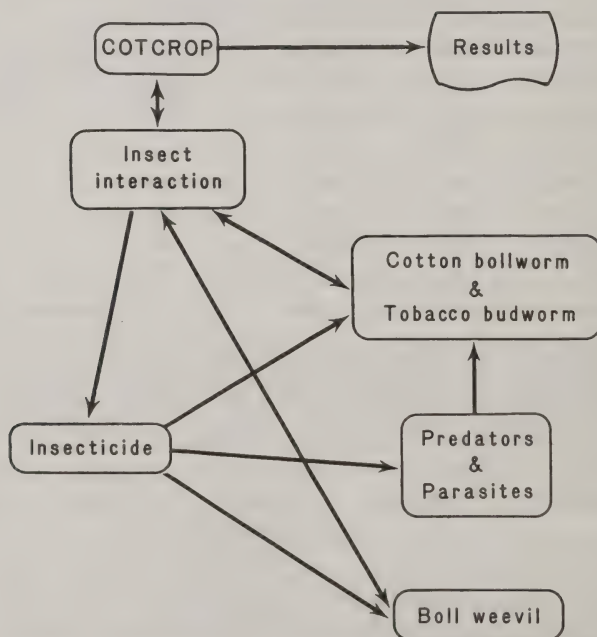
Figure 3. Schematic of coupled simulation models of the cotton crop, *Heliothis* spp., boll weevil populations, and beneficial insects.

Cotton Model

COTCROP is a dynamic cotton model developed by Jones et al. (1980). Crop growth is simulated for cotton plants growing on 1 m² ground area. Using maximum and minimum temperatures, solar radiation, pan evaporation, and existing water and nutrient balances, the model calculates the growth of the plants for each day. Carbohydrate and nitrogen balances are maintained in the plant, while nitrogen and water levels are updated daily in the soil. Initialization data required by the model include date of plant emergence, date of harvest, plant density, the amount and date of any nitrogen applications and irrigations, as well as soil parameters.

Each day nitrogen and carbohydrate demand is calculated based on the morphogenesis of the plants. The amount of carbohydrate available is determined from the carbohydrate reserves in the plant and the photosynthate produced that day. Available nitrogen and water are a function of both the rooting depth of the plants and the distribution of nitrogen and water in the soil. If the daily nutrient demand exceeds supply, the rate of organ initiation and growth rates of existing organs are reduced until the nutrients available can meet the demands. Any surplus of nitrogen or carbohydrate is stored in the plant for later use. Shortages of carbohydrate, nitrogen, or water will cause fruit to be tagged for abscission. Tagged fruit stop receiving nutrients after 3 days and fall from the plant after 5 days.

The soil profile is divided into 10-cm layers down to the maximum rooting depth. Water and nitrogen balances are calculated and distributed accordingly through the soil layers.

Water is redistributed throughout the soil profile after the amount of infiltration, evaporation, transpiration, and drainage for that day has been calculated. Similarly, nitrogen balance calculations for the various layers are based on nitrogen added to the soil by rainfall and organic decomposition, and by applications of nitrogen fertilizers. Nitrogen is removed from the soil via denitrification and leaching.

COTCROP maintains the number, weight, age, and nitrogen content of all the fruit on the plant. Each day this information is transferred to the insect models where damage from feeding and ovipositing is determined.

Boll Weevil Model

The boll weevil model is a modified version of the model BWSIM developed by Jones et al. (1975). Boll weevil population dynamics are affected primarily by daily temperatures and available diet.

The model is initialized with the number of adult weevils emerging from overwintering. The overwintering rate may be varied to produce various population levels.

The developmental unit concept (Jones et al. 1975) is used to move the weevils through the egg, larvae, pupae, pre-oviposition, and adult stages. Each day, hourly temperatures are used to calculate the elapsed developmental units for that day. The weevils in each life stage then progress through the various stages according to the number of developmental units to which they have been exposed. The number of weevils is reduced according to natural mortality factors, the number of adults entering diapause, and insecticides.

The maximum number of eggs laid by the adult females is calculated as a function of the average daily temperature. This amount is then reduced according to age and available diet and is distributed between the number of squares and bolls in the field. The total damage due to feeding and egglaying is transferred to the cotton model to schedule the abscission of fruit.

Heliothis Model

The *Heliothis* model was developed by Brown and Hogg and includes *H. zea* and *H. virescens* (Hogg and Calderon 1979)[a]. Because they have different rates of development and react differently to selected insecticides, the two species are kept separate in the model. The model is initialized with the number of adults entering the field in the spring. As in the boll weevil model, this number can be varied to produce the desired population levels.

The number of *Heliothis* in each life stage is maintained in separate arrays for eggs, larvae, pupae, and adults. Movement through the various life stages is temperature-dependent and is based on a degree-day development scheme from field data (Hogg and Calderon 1979).

Fecundity is a function of daily temperatures and the age of the adult. The fecundity function used is from Hartstack (1973).

Heliothis mortality may result from insecticides, predators and parasites, and from other natural effects. Insecticide kill has varying degrees of effectiveness, depending on physical factors in the environment and the age and species of each insect. Insecticide applications have a residual effect for up to three days. Predaceous and parasitic insects feed on eggs and larvae. Thus the mortality is proportional to the number of predators and parasites present. The level of predators and parasites is treated as an exogenous variable, subject to the effects of insecticide applications. An insecticide application reduces the level of predators by 80% and recovery occurs at a linear rate over a period of 14 days.

The damage done to the cotton crop by *Heliothis* is caused by larval

[a]Field developmental times of *Heliothis zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) larvae and pupae in cotton. Unpublished.

feeding on squares and young bolls. Data collected by Townsend (1974) were used to estimate the number of fruit eaten per larva per day. Whereas small larvae (1–4 days old) feed on small squares (1–16 days old), large larvae (17 days old or older) feed on all squares and bolls up to 20 days old (Brown et al. 1976). The feeding damage is transferred to the cotton model where fruit is scheduled for abscission.

Coupled Models

With the models interfaced as shown in Figure 3, the status of the cotton crop and insect populations is updated on a daily basis and the simulation may be carried out through part or all of the growing season. The timing of insecticide applications may be set up on a fixed schedule or programmed in terms of scouting interval, damage thresholds, or insect level thresholds. The output of the model includes a daily record of crop status and daily levels of all stages of insect development. At the end of the growing season, a summary report gives the final yield, number and cost of insecticide applications, and returns above the cost of insect control.

METHODOLOGY

The probability of zero, low, medium, and high populations of boll weevils, *Heliothis*, and beneficial insects was established for the two major cotton-producing regions of the state of Mississippi (Table 3). The joint probabilities are reported in Table 4. Specific levels to be simulated for

Table 3. Probability of zero, low, medium, and high insect populations, in major cotton-producing regions of Mississippi, USA

Insect population level	Probability (%)		
	Boll weevil	*Heliothis* spp.	Beneficials
Delta region			
Zero	75	0	0
Low	15	40	55
Medium	10	45	35
High	0	15	10
Non-Delta region			
Zero	0	0	0
Low	25	55	5
Medium	55	35	40
High	20	10	55

Table 4. Probability of selected levels of insects, by region, Mississippi, USA

Insect population[1]			Probability of occurrence	
Boll weevil	*Heliothis* spp.	Beneficials	Delta region	Non-Delta region
O	O	O	0.0	0.0
O	O	L	0.0	0.0
O	O	M	0.0	0.0
O	O	H	0.0	0.0
O	L	O	0.0	0.0
O	L	L	0.165	0.0
O	L	M	0.105	0.0
O	L	H	0.030	0.0
O	M	O	0.0	0.0
O	M	L	0.165	0.0
O	M	M	0.105	0.0
O	M	H	0.030	0.0
O	H	O	0.0	0.0
O	H	L	0.0825	0.0
O	H	M	0.0525	0.0
O	H	H	0.015	0.0
L	O	O	0.0	0.0
L	O	L	0.0	0.0
L	O	M	0.0	0.0
L	O	H	0.0	0.0
L	L	O	0.0	0.0
L	L	L	0.033	0.0
L	L	M	0.021	0.056
L	L	H	0.006	0.084
L	M	O	0.0	0.0
L	M	L	0.033	0.0
L	M	M	0.021	0.016
L	M	H	0.006	0.024
L	H	O	0.0	0.0
L	H	L	0.0165	0.0
L	H	M	0.0105	0.008
L	H	H	0.003	0.012
M	O	O	0.0	0.0
M	O	L	0.0	0.0
M	O	M	0.0	0.0
M	O	H	0.0	0.0
M	L	O	0.0	0.0
M	L	L	0.022	0.0
M	L	M	0.014	0.168
M	L	H	0.004	0.252
M	M	O	0.0	0.0
M	M	L	0.022	0.0
M	M	M	0.014	0.048

Insect population[1]			Probability of occurrence	
Boll weevil	*Heliothis* spp.	Beneficials	Delta region	Non-Delta region
M	M	H	0.004	0.072
M	H	O	0.0	0.0
M	H	O	0.0	0.0
M	H	L	0.011	0.0
M	H	M	0.007	0.024
M	H	H	0.002	0.036
H	O	O	0.0	0.0
H	O	L	0.0	0.0
H	O	M	0.0	0.0
H	O	H	0.0	0.0
H	L	O	0.0	0.0
H	L	L	0.0	0.0
H	L	M	0.0	0.056
H	L	H	0.0	0.084
H	M	O	0.0	0.0
H	M	L	0.0	0.0
H	M	M	0.0	0.016
H	M	H	0.0	0.024
H	H	O	0.0	0.0
H	H	L	0.0	0.0
H	H	M	0.0	0.008
H	H	H	0.0	0.012
			100%	100%

[1] O = zero; L = low; M = medium; H = high population level.

Heliothis and beneficials are given in Figures 4 and 5. Corresponding information for boll weevils, is reported in Figure 6.

Agronomic events or data such as day of emergence, day of harvest, date and amount of fertilizer applications, and soil parameters were fixed by region. Insect control threshold values simulated were fixed at the levels recommended by the Mississippi Cooperative Extension Service. Insect populations were varied as appropriate to reflect the probabilities reported in Table 4. To overcome the problem of yearly variations in weather, each simulation was made with 4 years of weather data, the sets being selected to reflect the range of weather typically experienced in Mississippi.

Not all possible combinations of boll weevils, *Heliothis* spp., and beneficials (see Table 4) were run; only those combinations with a high likelihood of being observed were run. Pairs of runs of particular interest had fixed levels of boll weevil and *Heliothis* spp. and varying levels of beneficials.
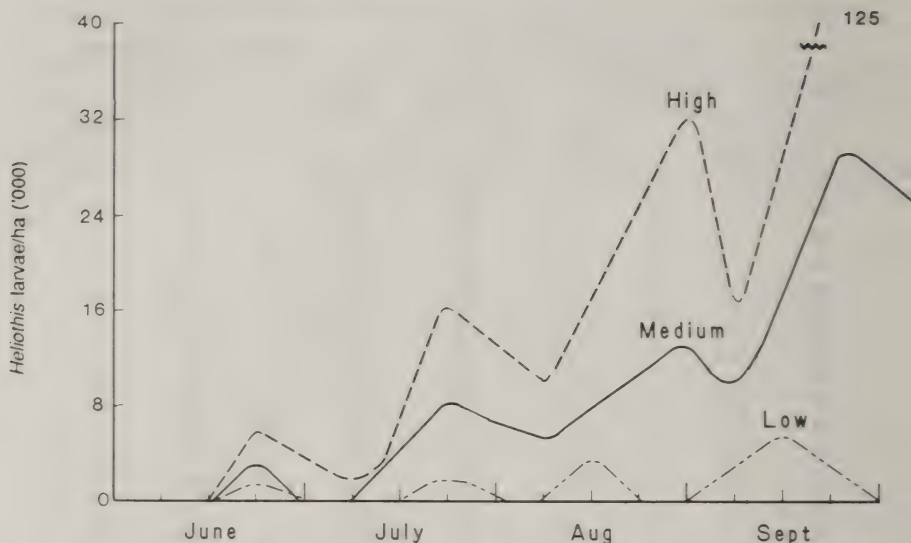
Figure 4. High, medium, and low *Heliothis* larval populations on cotton in the U.S. midsouth.

A thorough description of simulating the interrelationships between the cotton crop and insects is given by Brown et al. (1979). The specific methodology employed in this study is described in detail by Murphey (1980).
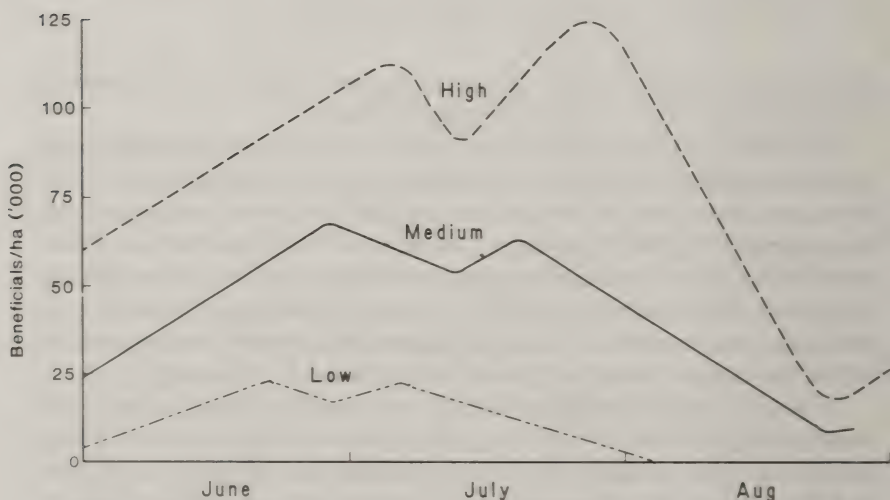
Figure 5. High, medium, and low beneficial insect populations on cotton in the U.S. midsouth.
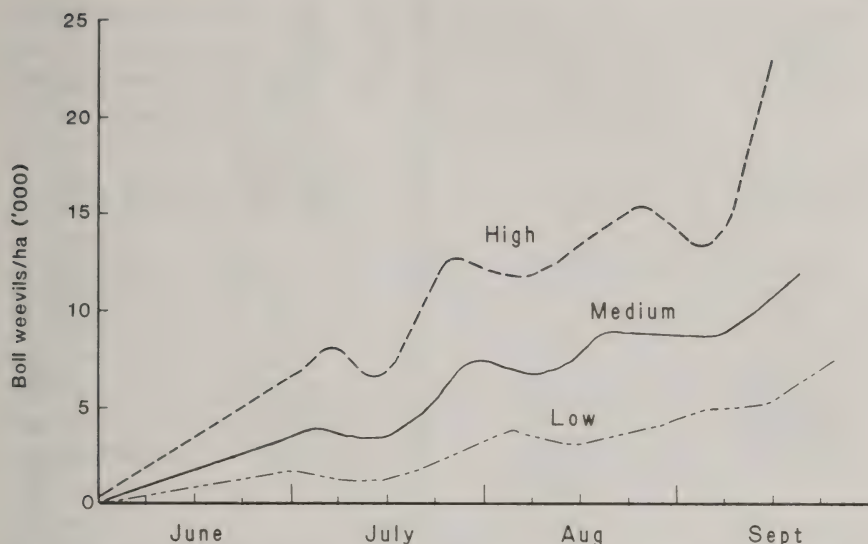
Figure 6. High, medium, and low boll weevil populations on cotton in the U.S. midsouth.

RESULTS

The results of the 24 simulation runs per region were averaged over years. The results for the Delta and non-Delta regions are summarized in Tables 5 and 6, respectively. Simulated yields and number of insecticide applications are consistent with current information concerning their absolute size and relative differences.

In the Delta, increasing the level of beneficials from low to medium increased yield by 9.1 to 30.3 kg of lint per ha and reduced the number of insecticide applications by 0.50 to 1.50 applications per season.

In the non-Delta, increasing the level of beneficials from medium to high increased yield by 2.7 to 4.6 kg of lint per ha and reduced the number of insecticide applications by 1.25 to 1.50 applications per season.

An examination of specific insecticide application dates (not reported) revealed that the addition of the boll weevil to the non-Delta agroecosystem prohibited the beneficial insects from having as large an impact in the non-Delta as they did in the Delta.

Approximately 70% of the joint probabilities were simulated in each region. Assuming that the 30% not simulated do not alter the average, the average economic value of beneficial insects is approximately $43.47 per ha on commercial cotton in the Delta and $27.91 per ha in the non-Delta (assumes the following prices and cost: cotton lint $1.48 per kg, cotton seed $181.40 per metric ton, insecticide $16.67 per ha per application).

These results compare favorably with the findings reported by Lin et al.

Table 5. *Average simulated yield of cotton lint (kg/ha) and number of insecticide applications, Delta region of Mississippi, USA, 1962, 1968, 1969, 1972*

Insect population level[1]	Probability	Cotton yield (kg/ha)	Insecticide applications (no.)	Average difference in yield (kg/ha), M-L beneficials	Average difference in insecticide application no., M-L beneficials
OLL	0.165	775.2	7.75	—	—
OLM	0.105	785.0	6.25	9.8	1.50
OML	0.165	767.1	7.50	—	—
OMM	0.105	797.4	7.00	30.3	0.50
OHL	0.0825	747.2	8.50	—	—
OHM	0.0525	756.3	7.50	9.1	1.00

[1]Boll weevil, *Heliothis* spp., and beneficials, respectively. O = zero population level; L = low; M = medium; H = high.

Table 6. *Average simulated yield of cotton lint (kg/ha) and number of insecticide applications, non-Delta region of Mississippi, U.S.A., 1962, 1968, 1969, 1972*

Insect population level[1]	Probability %	Cotton yield (kg/ha)	Insecticide applications (no.)	Average difference in yield (kg/ha), H-M beneficials	Average difference in insecticide application no., H-M beneficials
LLM	0.056	586.9	6.00	—	—
LLH	0.084	589.6	4.50	2.7	-1.50
MLM	0.168	551.3	6.50	—	—
MLH	0.252	555.9	5.25	4.6	-1.25
MMM	0.048	555.4	7.50	—	—
MMH	0.072	558.9	6.25	3.5	-1.25

Boll weevil, *Heliothis* spp., and beneficials, respectively. L = low population level; M = medium; H = high.

(1980) in an econometric analysis of the impact of insecticides and beneficial insects on cotton yield. The results are essentially identical to the results given by Murphey (1980) in a study of alternative cotton insect control strategies employing the identical methodology.

LIMITATIONS

Simplifying assumptions necessarily limit the interpretation of the results. Beneficial arthropods are comprised of predators and parasites. The simulations were made without parasites. Five to ten years ago this might not have been viewed as a serious limitation. However, recent information indicates that the insecticide materials of choice for *Heliothis* control in the midsouth (pyrethroids) are less selective for parasites than organophosphates (Powell et al. 1986), that relative numbers of parasites are increasing, and that they may be contributing to our recent lack of problems with *Heliothis* (King et al. 1985). The failure to include beneficial parasites probably biased downward the estimated economic value of beneficial arthropods.

The simulation did not consider the impact of plant bugs. These pests primarily impact cotton in the midsouth during the early season. Since no early-season pest was involved in the simulations for the Delta region, the estimate of the economic value of beneficials is probably biased upward for the Delta region.

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Distribution of *Heliothis* and Their Natural Enemies and Host Plants

Introduction

L. Knutson and *S. Nagarkatti**

Effective, economical, environmentally sound, and energy-conservant control of *Heliothis* will be achieved only through the integration of biological control with other pest management approaches. Successful integration of biological control with other control methodologies depends on the quality and extent of our knowledge of fundamental areas such as biosystematics, distribution, host plants, kinds and range of natural enemies, and economic impact worldwide. These areas are reviewed and analyzed in this subtopic.

We will first provide a biosystematic background for research on *Heliothis* and its natural enemies because this information is fundamental to any major pest management enterprise. That is, we will describe the "state of the art" of *Heliothis*/natural enemy biosystematics and highlight areas where further research is needed, is possible, and would be productive. We will also bring together biosystematic information of a practical nature of value to researchers in biological control: names and address of taxonomists, reviews of collections as sources of information and of recent literature, and other useful data arranged for the convenience of the researcher.

We will next provide a summary of the classification of *Heliothis* and the genus *Helicoverpa* as first proposed by D.F. Hardwick. This is crucially important, because classifications may provide highly predictive clues, guidelines, and insights into the relationships among the species of *Heliothis* and *Helicoverpa* that can be used to direct and evaluate research questions. In the chapters by Poole and Knutson, the taxonomy and nomenclature of *Heliothis* and *Helicoverpa* are discussed and the controversy over the use of the names and the preference of the workshop participants to use *Heliothis* are discussed. The relationships of *Heliothis* with related genera have been fairly well studied, although not completed. Biologists ignore this base of data at their own peril. Although major changes in names create operational and communication problems, the

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need is very real for an accurate understanding of phylogenetic relationships which have important implications for biological control. Therefore, we have asked the taxonomists to provide us with the facts as presently known.

Once we have gained the necessary systematics background, we can begin to bring together other basic information on distribution, host plants, and natural enemies on a regional/country basis for North and South America, Western Europe, Southern and Eastern Africa, Egypt, Pakistan, India, China, Southeast Asia, and Australia. The worldwide distribution of economically important *Heliothis* is summarized in Table 1. *Heliothis* contains over 50 species, including some of the most economically important insect pests in the world. *Armigera* (Hübner) and *zea* (Boddie) (bollworm or corn earworm) are perhaps the most infamous of these species. Until about 1953 they were considered the same species; in fact, these two species mate and fertile progeny may be produced. *Armigera* and *zea* are distributed worldwide between 40–45° N and 40–45° S of

Table 1. *Worldwide distribution of some economically important* Heliothis

Geographic zone	*Heliothis* species						
	armigera	zea	virescens	punctigera	viriplaca	assulta	peltigera
Palearctic							
Europe	++						0
USSR	+++				0		0
PRC	+++					0	0
Asia							
Southwestern	+++				+++		++
Southeastern	+++					+	0
Africa							
Northern	+++						0
Southern	+++					+	0
Oceania							
Australia	+++			+++		0	
Nearctic							
Canada, USA,							
Mexico		+++	+++				
Neotropical							
Central and South							
America		+++	+++				

0 = Nonpest.

+ = Occasional pest.

++ = Annual pest causing moderate damage.

+++ = Annual pest causing severe damage in absence of insecticides.

the Equator. *Armigera* is considered to be a major pest of crops such as cotton and tobacco in southern Europe (Spain, Portugal, Turkey, and Greece); southern Asia, (China, India, and Thailand); southern and eastern African countries; and in Australia. *Zea* and *virescens* (F.) (budworm) are major pests of a wide range of crops in North, Central, and South America. However, *Heliothis punctigera* Wallengren is largely restricted to Australia, where it is a major pest of cotton. Other pest species of minor importance include *gelotopoeon* (Dyar) in South America, *viriplaca* (Hufnagel) in southern Europe, *assulta* Guenee and *peltigera* [Denis and Schiffermüller] in southern Asia, and *nubigera* Herrich-Schäffer and *fletcheri* (Hardwick) in Africa.

Host plant records for *Heliothis* are summarized in Table 2. Certainly *armigera, punctigera, zea,* and *virescens* do not suffer from a narrow host range; each of these species feeds on over 100 different plant species. Field crops attacked are some of the world's most important and include corn, cotton, sorghum, soybeans, vegetables, and tobacco throughout the world. Pulse crops are the primary source of protein for predominantly vegetarian India, and these plants are heavily attacked by *H. armigera.* Other species such as *assulta* attack tobacco in southern Asia. *Viriplaca* and *peltigera* attack safflower in Syria and Iran, and *fletcheri* attacks sesame in the Sahel of Africa. Another species, *gelotopoeon,* is often reported to attack cotton in South American countries, e.g., Argentina.

Table 2. Number of host plant records for Heliothis

Country	*Heliothis* species				
	armigera[1]	*punctigera*	*zea*[2]	*virescens*[2]	*assulta*
India	150				
Australia[3]	75	120			Solanaceous plants
USA			100	100	

[1]Reed and Pawar (1982) reported that *H. armigera* damaged 60 cultivated plant species and at least 67 other plant species in 39 families across Africa, Asia, and Australia.

[2]Stadelbacher et al. (unpublished S-59) listed 70 wild hosts for *H. zea* and 76 wild hosts for *H. virescens* in the U.S. Quaintance and Brues (1905) listed cultivated species that were damaged by *Heliothis.* Tietz (1952, A manual of the Lepidoptera of Pennsylvania. Pennsylvania State College, School of Agri., State College, PA. 194 pp.) lists about 100 hosts for *H. zea* and about 30 for *H. virescens.*

[3]Based on Twine (these Proceedings).

In the USA, it has been estimated that the bollworm or corn earworm and the tobacco budworm may cause as much as $1.25 billion damage to crops annually in spite of insecticide application costing another $250 million per year. These figures are high but not extraordinary; damage

estimates to chickpea and pigeonpea alone in India are $200–400 million/ year. Damage estimates to cotton by *Heliothis* in Australia approximate those in the USA on a per unit basis. One commercial U.S. firm has reported that more insecticides are applied to control *Heliothis* than to control any other insect pest.

Although natural enemy data are not easily summarized, the nine regional papers included here provide a wealth of information on the subject. Several other papers in the workshop also present information on natural enemies and pathogens. For the latter, see especially the papers by Teakle, Carner and Yearian, and Jayaraj et al.

With such basic information in hand, we are in a position to interrelate the various subtopics of the workshop, to assess opportunities for establishing new natural enemies, and finally, to make specific recommendations. These recommendations are reported separately, following the preface.

Systematics of *Heliothis* Species and Their Natural Enemies as a Basis for Biological Control Research

*L. Knutson**

ABSTRACT

The rationale is discussed for biosystematic input into research and application programs on biological control of *Heliothis* (including the subgenera *Heliothis* and *Helicoverpa*). Biosystematic approaches are enumerated, and current research on genetic structure of species and populations is summarized. The status is summarized of current taxonomic knowledge of the major groups of natural enemies (Tachinidae, Braconidae, Chalcidoidea, Trichogrammatidae, Hemiptera, Ichneumonidae, predatory wasps, Coccinellidae, and Chrysopidae) of *Heliothis*. An international cooperative research effort on biosystematics of *Heliothis* and natural enemies is described. The taxonomic expertise and collection resources, including a directory of systematists and of collections relevant to *Heliothis* and major groups of natural enemies, are assessed on a regional basis.

INTRODUCTION

Research on biological control of *Heliothis*[1] should be approached from the broad context of habitat manipulation. The pests themselves and their biological control agents are the focus of this workshop and of similar analysis and planning sessions, but there are many other biotic elements in the agroecosystems that we manipulate. We especially need to consider major pest management programs in the context of the productivity of the broad agroecosystems *and* the health of the natural ecosystems on which these agroecosystems have been imposed.

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[1]As the taxonomic status of *Heliothis* Ochsenheimer and *Helicoverpa* Hardwick is not completely resolved, I am, in this paper, using *Heliothis* as the nominate genus, including *Heliothis* (in the strict sense) and the often recognized *Helicoverpa* as subgenera. The subgeneric names are used only where supraspecific distinction may be useful.

Different research projects and habitat management procedures have different needs for information about their associated plant and animal components. These needs generally start with the question, "What is it?" Our ability to answer such a question *authoritatively* is highly unpredictable because baseline information on plant and animal inventories is woefully inadequate in all areas where major pests, e.g., *Heliothis,* are problems. Although the diversity of plants and animals in temperate areas is somewhat better known than in tropical regions, the level of knowledge is still far from adequate. Not only are the current biosystematic services inadequate to meet the needs, but in many countries the necessary organizational structures are not in place or are inadequately involved in overall pest management activities.

These structures include national biological surveys, national systematic biology units, and/or research arms of national natural history museums. For example, only in the past few years has there developed a broad consensus among the systematics community and some user groups in the USA that a national biological survey, a complete analysis of the identity and distribution of all plants and animals, is a national imperative. The *international* mechanisms for expediting cooperation and obtaining support are poorly established. The International Work Group on Biosystematics of *Heliothis* and Arthropod Natural Enemies, which developed from the symposium on biosystematics services at the 1984 International Congress of Entomology (described later in this paper) was formed specifically to establish such international mechanisms.

Suppliers of "systematics" information probably have a more intimate relationship with biological control workers than with workers in any other group. In fact, there is a true symbiosis between systematics and biological control (Knutson 1981). These interactions are summarized in Table 1. The many papers written by biological control specialists and systematists on the relationships between these areas are given in an updated list of publications included as a separate section in the bibliography of this paper. However, to date no overview has been presented of the biosystematic needs of research and action programs on biological control of *Heliothis* by natural enemies. Needs for taxonomic, systematic, and biosystematic research and services for *Heliothis* and associated natural enemies are diverse and extensive, and unpredictable. The needs range from brief but critical input at certain stages of a project to continuing, long-term requirements. Biological control by natural enemies is the heaviest user area of biosystematics, followed by pest survey work. Some other major aspects of research and application that require biosystematic investigations and services are: port-of-entry surveillance, prediction of potential new pests, studies of aestivation-hibernation-diapause, analyses of population ecology, host-range studies, determinations of susceptibility to

Table 1. Biological control biosystematics matrix: introduction of foreign natural enemies

Biological control activities	Primary capabilities needed	Kind of biosystematic data	Format of biosystematic data	Biosystematic resource requirement(s)
Project planning	Predictive capability	Comprehensive classifications of foreign hosts and enemies, geographical distribution, host and ecological data, biosystematics of target pests	Modern revisions and monographs of foreign natural enemies	Extensive literature, collections, expertise, knowledge of endemic natural enemies
Foreign exploration	Field and laboratory identification of limited natural enemy groups and host groups	Identification aids to foreign faunas and floras	Foreign faunistic studies, field guides	Immediate, broadly capable identification services
Foreign prequarantine selectivity studies				
Domestic quarantine and selectivity studies	Cryptic species and infra-species recognition	Biosystematic studies	Biosystematic studies with identification aids	Biosystematists with morphological expertise
Research (postquarantine)	Cryptic species and infra-species recognition	Biosystematic studies	Basic papers and in-depth guides to literature	Biosystematics expertise
Field release	Ecosystematic data; microhabitat selection	Ecosystematic data and advice	Publications, data banks, personal communication	Field-oriented systematists
Evaluation and impact studies	Field and laboratory identification of natural enemies, alternate hosts, hyperparasites, and other associates	North American faunistic studies; comprehensive classifications of hosts and alternate hosts	Modern, North American revisions, monographs; specialized training; handbooks	Highly expert identification screening system

Source: Knutson 1981.

pesticides, long-distance migration and mesoscale movement studies, field-testing of pheromones, evaluation of the environmental impact of control measures, development of genetic control methods (especially backcross sterility in *H. zea*), and development of cultural control procedures.

TAXONOMY, SYSTEMATICS, BIOSYSTEMATICS

It might be useful at this point to clarify some possibly confusing terminology, specifically "taxonomy," "systematics," and "biosystematics." The needs for information on *Heliothis* and natural enemies are mostly along the lines of biosystematics, but all three are involved. The dividing lines between taxonomy, systematics, and biosystematics are not sharply defined, and the terms are often used synonymously. However, *taxonomy*, or "alpha-taxonomy," is most correctly used to describe the traditional, morphologically based procedures for development of classifications that, while they may have some predictive value, are by and large constructed to enable identification. Biological data may be used in developing such classifications, but such data generally are rather limited and usually consist of specimen label data.

The science of *Systematics* includes basic research on classifications but is generally considered to differ somewhat from taxonomy in methodology and application and is directed in part toward answering more general evolutionary questions. Data used often include biogeographical and biological information; data analyses often involve cladistic (classification based on deduced relationships) or phenetic (classification based on overall similarities and differences) interpretations in the attempt to develop predictive classifications. The results are often applied to major questions of evolutionary biology.

Biosystematics is a more recent term and generally involves the study of the living organism. A primary objective is the development of predictive classifications. Predictive classifications are those that permit one to postulate the state of unknown characteristics and characters, because the classification is based on descent; that is, classifications that can be used to project key biological aspects (e.g., hosts/prey) of a biologically unknown taxon based on its classificatory relationship to a biologically known taxon. These are particularly useful to researchers in other areas. Experimental methodologies such as cross-breeding, electrophoresis, and field research on hosts and natural enemies are often carried out as a part of biosystematics research. Characterization of species at the population level and elucidation of predictive phylogenetic relationships are basic objectives of biosystematics.

In general, taxonomic-systematic-biosystematic data on *Heliothis* and its natural enemies will be derived from some combination of the following approaches and methodologies which are appropriate at the species or population levels:

I. Morphological methodology (adults and immatures)
   A. Light microscope
   B. Stereoscan electron microscope
   C. Computer-assisted image analysis
   D. Statistical, phenetic, and/or cladistic data analyses
II. Biochemical and molecular methodology (primarily used to develop population genetic data and estimate phylogenetic distances)
   A. Isozyme-allozyme analysis (electrophoresis)
   B. Protein analysis (high performance liquid chromatography)
   C. Cuticular hydrocarbon analysis
   D. Immunology-microcomplement fixation
   E. Amino acid sequencing and DNA hybridization
   F. Chemoprint (elemental) analysis
III. Traditional genetics
   A. Cross-mating experiments
   B. Karyology (number, morphology)
   C. Gametogenesis
IV. Behavior (mating, migration, host location, oviposition, larval feeding, etc.)
V. Physiology (diapause, pheromones, host-plant chemistry, etc.)
VI. Ecology
   A. Geographical and habitat distribution
   B. Host plants, including reservoir hosts
   C. Natural enemies, including pathogens
   D. Phenology

Specific biosystematic research needs will be discussed within the context of a new plan for an international cooperative research effort on the biosystematics of *Heliothis* and its natural enemies.

GENETIC STRUCTURE OF SPECIES AND POPULATIONS

Biological control by natural enemies requires information on the identity of the control agents, and often pests, that ranges from the kinds of data provided by classical, morphologically based taxonomy to information on the genetic structure of populations and species obtained from molecular biological approaches.

Of the various parameters used to characterize populations, morphological, behavioral, and ecological parameters are usually of the most

limited use for describing genetic structure because the genetic control of these characters is not well understood. Multivariate analyses of morphological characters, however, can provide a means of differentiating populations. Immunogenetic methods are often not useful for defining populations because technical difficulties limit their large-scale application.

Electrophoretic analysis of allozyme variation and restriction endonuclease analysis of DNA variation are currently the most useful techniques for population analyses. Allozyme analysis has been conducted for hundreds of species and for most taxonomic groups. However, direct estimates of nucleotide sequence divergence have been made for relatively few species pairs. Both of these methods allow us to (1) use variants of a purely genetic nature (i.e., differences in amino acids in electrophoretic analysis and nucleotide sequences in restriction endonuclease analyses) and (2) measure the genetic make-up of individuals at large numbers of loci or nucleotide sites. We can expect that routine methods for large-scale DNA sequencing will eventually replace these methodologies for all but population level studies.

Allozyme analysis by electrophoresis and specific histochemical staining, often combined with genetic and morphological procedures, is being used extensively in the study of Trichogrammatidae and, to a limited extent, of *Heliothis* and *Helicoverpa*. At the 1981 "International Workshop on *Heliothis* Management" it was recommended that to determine the presumed subspecies of *Heliothis* (*Helicoverpa*) *armigera* and their geographical ranges, ". . . either the live insects or acetone-extracted materials should be sent to a central laboratory for testing" (Lingren 1982).

The biochemical technique of allozyme electrophoresis is useful both for the identification of species and in studies of natural genetic variation, and gene flow in populations. It is perhaps the most powerful technique currently available for defining the limits of species' populations. Sluss et al. (1978) and Sluss and Graham (1979) studied genetic variation in *Helicoverpa zea* and *Heliothis virescens* in the United States. More recently, Daly and Greg (1985) studied *Heliothis* (*Helicoverpa*) *armigera* and (*H.*) *punctigera* in Australia to provide background information relevant to study of the evolution of pesticide resistance. They established seven useful loci and were able to distinguish all life stages, including single eggs and the early instar larvae of both species, and showed that the traditional criteria for distinguishing later instar larvae were not reliable. Their estimation of the genetic distance between *Heliothis* (*Helicoverpa*) *armigera* and (*H.*) *punctigera* as compared to the genetic distance between *Heliothis virescens* and *Heliothis* (*Helicoverpa*) *zea* (determined by Sluss et al. 1978) correlates with Hardwick's (1965) separation of *Heliothis* and *Helicoverpa* by morphological characters.

Relationships between species of *Heliothis* and *Helicoverpa* also may

be established by use of some of the newer molecular biosystematic approaches. As an example of these approaches, Dr. Milton Huettel of the Biosystematics and Beneficial Insects Institute in Beltsville, MD, has provided the following brief description of some of his recent work. Mitochondrial DNA (mtDNA) is being studied intensively because of its probable role in maternal inheritance male sterility in *Heliothis virescens* backcross hybrids. Lansman et al. (1979) demonstrated interspecific differences between *H. virescens* and *H. subflexa* in this molecule and the lack of any detectable paternal contribution, via sperm, to the mitochondrial DNA complement of the developing embryo. Mitochondrial DNA is mapped by digestion with a suite of restriction endonuclease enzymes. These enzymes cut the circular mtDNA molecule into linear fragments, which are then separated and sized on electrophoretic gels. Combinations of single, double, and partial digests are used to order the restriction sites along the molecule. Resulting maps can then be compared. Restriction maps of *Heliothis* (*Heliothis*) *virescens*, *H.* (*H.*) *subflexa* and *Heliothis* (*Helicoverpa*) *zea* and (*H.*) *armigera* are being prepared to assess their use in systematic studies. The mtDNA of (*H.*) *armigera* has been cloned. The availability of these clones will make possible examination of other less abundant species for systematic purposes.

One of the objectives of this study is to determine whether there are domains within the mtDNA molecule that will allow clustering of species within genera (conservative domains), and others that will be useful for distinguishing very closely related species (rapidly evolving domains). It will require study of a large proportion of the species of each genus to be able to say with reasonable certainty that *Heliothis* and *Helicoverpa* can be distinguished on the basis of one or more restriction sites. At present, we can only distinguish three North American species (*H. virescens, H. subflexa,* and *H. zea*), all of which originated from laboratory colonies. The *H. armigera* clones are being mapped now and will probably be distinguishable from the other three. We need good estimates of variation between individuals within populations and between populations (interspecific variability). Therefore, we are focusing at present on techniques that will allow us to analyze single individuals using the *armigera* clones as probes. We also need good samples of other species in both genera to develop a phylogeny.

Finally, analysis of proteins of certain species of *Heliothis* and *Helicoverpa* by use of high performance liquid chromatography, has recently been initiated by S. Ramaswamy and Dr. J. Baker at Mississippi State University.

All of these approaches, but biochemical genetic procedures particularly, require reasonable sample sizes from natural populations. All too often, strains are established in the laboratory from a very few wild caught

individuals and then studied and compared as though they were taxo-
nomic entities. This thinking and approach probably has led to many of
the taxonomic problems asserted to exist in biocontrol agents, such as
Trichogramma.

GENERAL STATE OF TAXONOMIC KNOWLEDGE, WITH RECENT, SPECIFIC REFERENCES

Brief summaries of current knowledge of the systematics of major groups,
and references to recent publications, are given below.

A. *Heliothis* and *Helicoverpa*: Relatively little research has been con-
ducted on the systematics of *Heliothis* and *Helicoverpa* since D.F. Hard-
wick's major papers in 1965 and 1970. Nye (1982) reviewed the nomencla-
ture of *Heliothis* and related taxa. The International Commission of
Zoological Nomenclature (Melville, 1985) ruled on Nye's (1980) applica-
tions and determined that the gender of *Heliothis* be considered feminine
(thus *H. armigera*, not *H. armiger*, etc., is correct) and the subfamily group
name Heliothinae (not Heliothidinae) is official. Nye (1982) noted, "My
own view as a museum taxonomist, but formerly an agricultural ento-
mologist, is that as generic boundaries are generally a matter of
opinion, depending on the user's tendency to lump or split, it is better to
have a broadbased genus *Heliothis* for the sake of field workers and to
divide it into subgenera such as *Helicoverpa* for the convenience of
taxonomists." He further noted, "Whether to use *Helicoverpa* to denote a
genus or a subgenus will always remain a decision for taxonomists and not
for the International Commission of Zoological Nomenclature." The
matter of *Heliothis* and *Helicoverpa* was discussed at the 1981 Workshop,
and it appeared that the majority of participants preferred not to recognize
two genera, although some believed there was value in recognizing two
subgenera, as suggested by Nye. The taxonomic evidence indicates that
Heliothis and *Helicoverpa* are distinct genera. Also, the recognition of two
genera would be important from the viewpoint of field workers who need
to be alerted to biological differences between the species, especially in the
corn earworm and tobacco budworm complexes.

However, there is need for more research on the higher classification of
the Heliothinae, including *Heliothis* and *Helicoverpa,* as shown by R.W.
Poole in his review of the systematics of *Heliothis* in these Proceedings.
The systematics of the adults of *Helicoverpa* and of the *H. virescens*
complex of *Heliothis* seem to be well known and little further work of the
classical type needs to be done. Adults of the remainder of *Heliothis*
species are not as well known because they are, as a rule, rare,
specialized, and of little or no real economic importance. The generic limits

of *Heliothis* and phylogenetic relationships within the genus are not well known, particularly for species found in tropical regions.

Another important taxonomic problem is the identification of larvae of *Helicoverpa* and *Heliothis*. Currently, the larvae of *Helicoverpa* cannot be separated from each other. A study of the systematics of the larvae and the production of identification keys is vitally important. The extensive rearing work necessary for research on the larvae could be expedited within the framework of an international cooperative effort such as that described later in this paper, on the International Advisory Council for Biosystematic Services in Entomology.

Recently, Mr. Marcus Matthews began a broadbased thesis research program at the British Museum (Natural History) and is conducting life-history studies in West Africa, especially on *Raghuva* Moore. He is working on a cladistic analysis of the Heliothinae, emphasizing the recognition of adults and larvae and relationships among the genera.

B. Tachinidae: Lack of identification capability for taxa in this family is a serious problem. The large number of species and poorly defined generic limits have been major obstacles to research in studies of the basic systematics of the family.

C. Braconidae: In North America, 15 species of Braconidae have been recorded as parasites of *Heliothis*, including four introduced species. Only three or four of these are important control factors. Marsh (1978) presented a key to North American braconid parasites of *Heliothis* and a list of Old World species records. Potential research needs are studies in the Old World, including Africa, and in Central and South America. The family is a good candidate for further research, especially the genera *Chelonus* and *Apanteles*.

D. Chalcidoidea: Few chalcidoids other than Trichogrammatidae attack *Heliothis*, with only three species recorded from *Heliothis* in the New World. Unknown chalcid species may attack *Heliothis* in the Old World. Many chalcidoids appear to be at least facultatively hyperparasitic on Tachinidae, Braconidae, and Ichneumonidae, and thus these species are of negative value to biological control. The Chalcidoidea parasitic on *Heliothis* do not need much taxonomic work unless surveys produce new host records.

E. Trichogrammatidae: Despite a great deal of study in recent years, the systematics of *Trichogramma* and *Trichogrammatoidea* are still not well understood. This difficulty has been partially solved with the application of male genitalia morphology and experimental hybridization techniques to *Trichogramma* biosystematics, beginning with the important studies of Nagarkatti and Nagaraja (1968, 1971, 1977). The designation of lectotypes

for several often misidentified species further clarified the taxonomy of *Trichogramma* in North America. Recently, the methods for investigating *Trichogramma* biosystematics have been further improved by the combination of studies of genital structure and hybridization experiments with isozyme analyses. Among the 20 species of *Trichogramma* known from the continental USA, *T. pretiosum* is the most common and widespread. Although *T. pretiosum* has been the subject of numerous biological studies and the species most frequently mass-reared for augmentative release programs, the exact identity of this important species is confused. Cross-breeding experiments indicate that the nominal *T. pretiosum* is probably comprised of several sibling species or distinct biotypes, and it is apparent that morphological analysis is not adequate for determining their identity (Hung et al. 1986).

F. Ichneumonidae: Catalogs for the regions of the world being considered in this workshop list 42 species of Ichneumonidae as primary parasites of 11 species of *Heliothis*. Recent revisions undoubtedly record additional ichneumonid parasites of those two genera. Of the 16 species recorded in America north of Mexico, only two, *Campoletis flavicincta* (Ashmead) and *C. sonorensis* (Cameron), appear to have an important impact on *Heliothis*. However, even for those two species, ecological preferences and host selection have been little studied, and none of the genera, including known parasites of *Heliothis,* can be considered well known taxonomically.

G. Heteroptera: Some Heteroptera or true bugs are nonspecific predators of *Heliothis* and *Helicoverpa*. Members of the anthocorid genus *Orius* [e.g., *insidiosus* (Say)] prey on the egg stages and perhaps, early instar larvae. *Nabis* spp. (Nabidae) and *Geocoris* spp. (Lygaeidae) feed on eggs and larvae. A few Miridae, including members of the genera *Ceratocapsus* and *Rhinacloa*, have been recorded as important predators of *H. virescens* in South America.

Identification of *Orius* is not very difficult. However, all of the New World Nabidae are in need of revision; studies on this group are under way by I.M. Kerzhner, Zoological Institute, Academy of Sciences, Leningrad, USSR. The Geocorinae of the eastern USA have been revised recently. Neotropical and the western U.S. species are very difficult, if not impossible, to identify with certainty. About the same situation exists in the Old World, with the European and Russian geocorine fauna much better known than the fauna of the African, southern Asian, Indo-Pacific, and Australian regions.

H. Predatory wasps: Wasps of the families Vespidae (especially *Polistes*) and Eumenidae are general predators of insects. Caterpillars are common prey, and most genera in the sphecid wasp tribe Ammophilini prey solely on caterpillars. None of these wasp groups have specific prey species—all

are generalists—and few studies have been made to assess their impact on pest populations.

Identification of species of Vespidae is fairly straightforward for yellow jackets and hornets worldwide, but identification of the approximately 250 members of the genus *Polistes* can be difficult. A revision of the North American species is needed. Richards (1978) prepared keys to the neotropical species, but identifications are not always easy or certain. The European *Polistes* have been treated in various regional works. However, except in Japan, the species in the rest of the Old World cannot be easily identified. Das and Gupta (1983) catalogued the Vespidae of the Indian subregion, but no identification keys were provided.

The taxonomy of the Eumenidae, a much larger group than the Vespidae, is basically in poor condition. There has been tremendous generic "splitting" without the accompanying keys to the generic taxa. Therefore, except in North America, it is often difficult or impossible to recognize the genus and, furthermore, the species of most genera have not been revised taxonomically. Consequently, species identifications are often difficult or impossible.

The genera of the sphecid tribe Ammophilini are well established. The New World members of the most important genus, *Ammophila*, are being revised by A.S. Menke, Systematic Entomology Laboratory, USDA, Washington, DC, who can supply identifications for most of the world fauna. *Podalonia*, a genus of the same tribe, whose species prey almost exclusively on cutworms, requires revision.

I. Chrysopidae: The green lacewings are predators on small, comparatively soft-bodied arthropods. Although aphids are the primary prey of most species, eggs and larvae of many Lepidoptera are readily accepted by some species. Certain species are very specific in terms of prey or habitattype, but others are very opportunistic feeders. *Chrysoperla carnea* (Stephens) is particularly well adapted to feed on a variety of prey on herbaceous crops, is easily reared in the laboratory, and has been used in control programs against *Heliothis*.

The identification of Chrysopidae to species is virtually impossible for most regions of the world, except by a few specialists with many years of experience. There are no general works for North, Central and South America, Asia, or most of Africa. Good recent revisions of the European (Aspöck et al. 1980), Australian (New 1980) and southern African (Tjeder 1966) fauna are available.

A broad range of information on Chrysopidae, with emphasis on actively developing areas of research and basic biology, was recently presented by Canard et al. (1984). The chapter on "Taxonomic problems" includes sections by T.R. New on "The Need for Taxonomic Revision in

Chrysopidae," by Y. Séméria on "Some Caryotypes in Chrysopidae," and by L. Bullini and R. Cianchi on "Electrophoretic Studies on Gene-Enzyme Systems in Chrysopid Lacewings." The introduction to T.R. New's section states:

> Chrysopidae have provided numerous problems for systematists. There is currently much confusion over generic allocation of many species, as well as uncertainty over some aspects of their subfamilial or tribal classification. The family incorporates some 1800 specific names for recent species, and these are distributed among nearly 90 genera or subgenera. Many undescribed taxa exist, and many of the described taxa are inadequately defined. Recent studies have tended to disclose numbers of synonyms: a current study of the New World fauna, for example, is almost halving the number of recognized species in that region (Adams 1978). A large proportion of the genera have been raised on the basis of single species (some on single specimens) and, whereas some of these are generally accepted, others are decidedly suspect as valid taxa. Classification has generally been based on a limited range of adult characters (see Chapter 2.2.), predominantly wing venation and colour, but more recently work has incorporated aspects of genitalic features and has emphasised that immature stages may also furnish valid systematic features. However, until recently, there has been insufficient appreciation of the extent of intraspecific variation in many adult features. The purpose of this brief account is to appraise the present state of chrysopid systematics, to comment on major lacunae in our understanding of the group, and to indicate zoogeographical aspects of the family. As Adams (1978) noted, Chrysopidae are both undercollected and understudied, so that conclusions may be open to severe revision in the future.
>
> There are no recent syntheses dealing with the whole of chrysopid systematics on a world basis, although several accounts have critically appraised the fauna of particular regions (Zimmerman 1957: Hawaii; Adams 1959: Micronesia; Kuwayama 1962: Japan; Tjeder 1966: South Africa; Hölzel 1967a: Asia; Aspöck et al. 1980: Europe; New 1980: Australia), have commented more generally on the higher classification of the family (Tjeder 1966; Adams 1978), or have synthesised data for particular subfamilies (Kimmins 1952: genera of Apochrysinae; Adams 1967: Mesochrysinae, Nothochrysinae; Hölzel 1970, Adams 1978: Chrysopinae).

In his review of the Chrysopinae (the largest subfamily, including about 1700 species in about 56 genera, and all species of interest to biological control), New notes:

○ "Although a few recent studies of larval form . . . may help in clarifying segregates of the '*Chrysopa* complex,' such data are not available for most species."

○ "Various attempts have been made to subdivide *Chrysopa* . . . into a series of subgenera or genera, and there has been much . . . discussion over the status and validity of some of these."

○ "Essentially, *Chrysopa* s.l. is so broad that it is difficult to make any meaningful generalizations about biology, distribution or phylogeny without its subdivision." Thus, the taxonomic situation is similar to that of *Heliothis sensu latu.*

○ "Killington's (1937)[2] plea for a world revision of *Chrysopa* is still timely."

A long-term, broad-scale research program on characterization of biotypes of Chrysopidae, especially *Chrysoperla carnea,* is being conducted by C.A. and M.J. Tauber at Cornell University, Ithaca NY, USA. They are emphasizing the definition of biological variation among biotypes, characterization and analysis of morphological variation among biotypes, correlations between biological and morphological variation, and establishment of criteria for selecting well-adapted biotypes.

J. Coccinellidae: There is little specific information on coccinellids as predators of Heliothinae, although many groups in the subfamily Coccinellinae are recorded as, at least occasionally, preying on Lepidoptera larvae.

INTERNATIONAL COOPERATIVE RESEARCH ON BIOSYSTEMATICS OF *HELIOTHIS* AND NATURAL ENEMIES

At the XVIIth International Congress of Entomology in Hamburg in August 1984, members of the Commonwealth Institute of Entomology; Biosystematic Research Institute, Agriculture Canada; and the Biosystematics and Beneficial Insects Institute, U.S. Department of Agriculture, organized a major symposium on "Biosystematics Services in Entomology." About 35 presentations were included, and the Proceedings of the Symposium are expected to be published shortly. A set of resolutions addressing the main issues of biosystematic services were drafted at the Symposium and were approved by the International Congress. Also, an "International Advisory Council for Biosystematic Services in Entomology" (IACBSE) was initiated at the Symposium. This Council has been formed, and specific steps are being taken to respond to certain well-recognized international needs by the time of the 1988 International Congress in Canada.

[2]Killington, F.J. 1937. A monograph of the British Neuroptera. 2. London. Royal Soc. 269 pp. + 15 pl.

Among the several items considered for immediate action, it was quickly recognized that international cooperative research efforts on the biosystematics of four groups, *Heliothis,* Tephritidae, and their natural enemies are primary needs. It was recognized not only that there are major, specific needs with regard to *Heliothis* and Tephritidae, but there are unique opportunities that would be especially meaningful to the success of the projects. That there are active working groups on both groups of organisms within the International Organization for Biological Control is particularly significant, and there could be useful linkages with these groups.

The objectives of the International *Heliothis* Biological Control Work Group are to (1) distribute a newsletter to provide a medium whereby biocontrol researchers of *Heliothis* can communicate; (2) serve as a basis for the exchange of information; and (3) serve as a basis for identifying and exchanging natural enemies. With these two working groups—and the planning, communication, and cooperation that will come out of this Symposium—an effective mechanism could be established for international cooperation in biosystematics of this most important group of pests and its biological control agents.

An entomologist in a developing country where these pests and natural enemies occur could make important contributions to biosystematics research, even if little specific systematics expertise is available for the groups in his or her country. For example, study material of *Heliothis,* host-plant information, geographical and habitat distribution information, and specimens of natural enemies and associated data are the kinds of essential resources that are needed and that can be contributed from all regions.

Draft Program: Work Group on Biosystematics of *Heliothis* and Their Arthropod Natural Enemies

Convenor

L. Knutson, Biosystematics and Beneficial Insects Institute, United States Department of Agriculture, Agricultural Research Service, Bldg. 003, Rm. 1, BARC-West, Beltsville, MD 20705 (tel. 301/344–3182).

Work group leader(s)

To be determined.

Objectives

To carry out specific, high-priority research and service projects relating to the biosystematics of *Heliothis* and its natural enemies (Tachinidae, Braconidae, Chalicidoidea, Ichneumonidae, Hemiptera, Coccinellidae,

Chrysopidae, predatory wasps, and spiders). Emphasis will be placed on projects that would benefit from international cooperation and that support other areas of work on *Heliothis*. Overall, the primary areas of current activity are biology, behavior, population ecology, biological control, host-plant resistance, and integrated control systems.

The following general and specific areas of interest/activity (not prioritized) have been identified to date. The postulated flow of information for biosystematic research on *Heliothis* and natural enemies is shown in Figure 1.

I.   Planning Information
    A.   Development of bibliographic database on biosystematics.
    B.   Assessment of current status of biosystematic knowledge and continued identification of general and specific research needs.
    C.   Directory of current research projects on biosystematics of *Heliothis* and their arthropod natural enemies.
    D.   Analysis of major research collections.
    E.   Directory of systematic specialists and sources of identification, with areas of expertise and interest.
II.   Collection of Material Needed for Systematics Research
    A.   Living and preserved material of *Heliothis* and *Helicoverpa* from Central and South America.
    B.   Host-associated arthropod natural enemies.
III.   Basic Systematics Research
    A.   Comprehensive, taxonomic studies, including descriptive and diagnostic work and predictive phylogenetics.
        1.   Cladistic analysis of genera of Heliothinae.
        2.   Generic revision of *Heliothis*. There are probably 75 species worldwide; the generic limits are poorly defined.
        3.   Phylogeny of *Helicoverpa*. The current classification is based on a small number of morphological characters. A search for additional morphological characters and use of biological data will be necessary to refine the Hardwick species-group hypothesis of phylogenetic relationships.
        4.   Holistic analyses of character systems of *Heliothis* and *Helicoverpa* using morphological, biological, biochemical, and molecular biological data in concert.
    B.   Analysis of infraspecific variation of the economically important, widely distributed species, especially of pest species, using morphological and molecular biochemical methodologies.
    C.   Population characterization of polytypic and sibling species.
    D.   Taxonomy of the larvae. (The larvae of most species are unknown).
IV.   Geographical Distribution
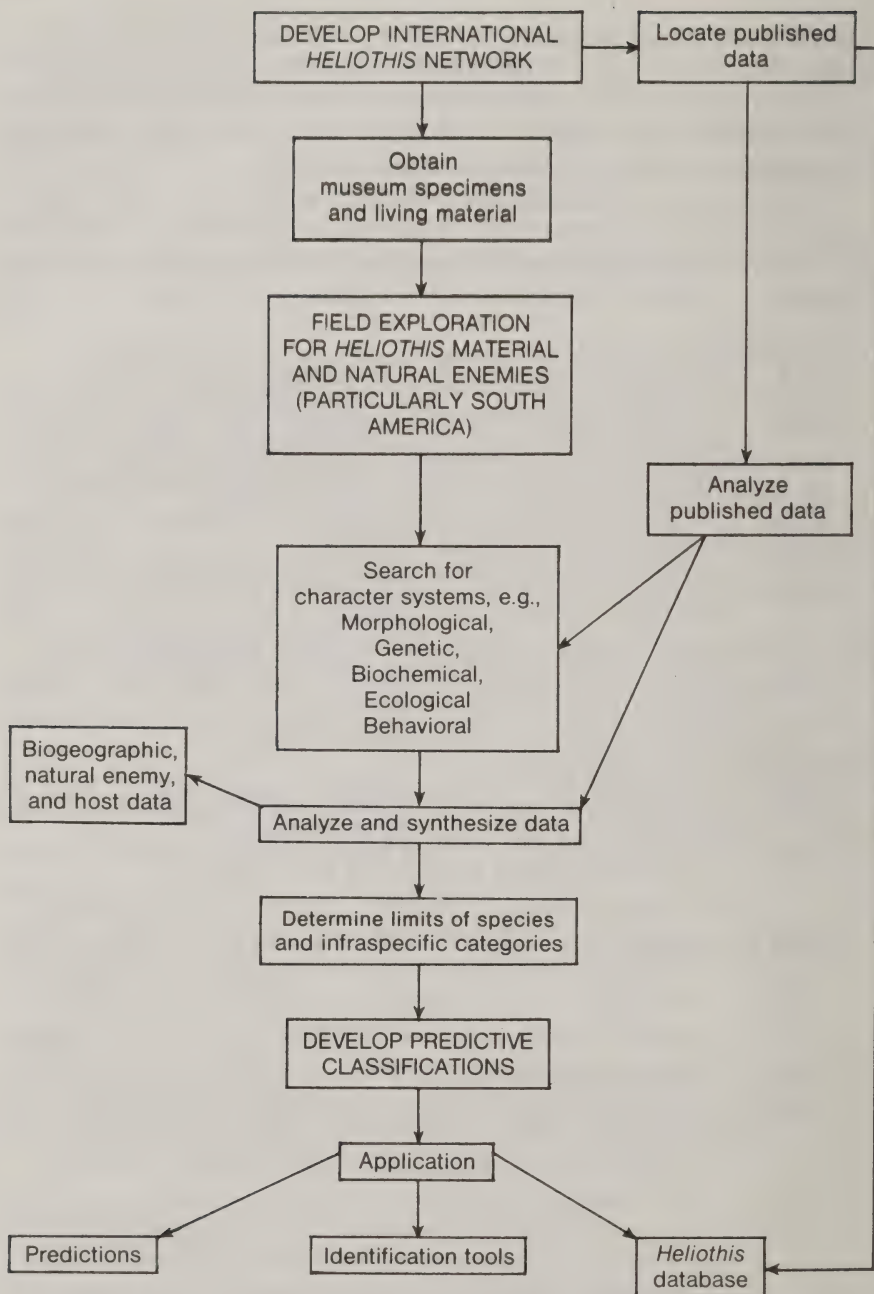
Figure 1. Flow of information for biosystematics research on *Heliothis* and other Heliothinae.

V. Habitat Distribution
VI. Host Plants (Wild or native host plants are unknown for most species).
VII. Natural Enemy Records
   A. Generalists
   B. Specialists
VIII. Production of a Newsletter (jointly with IOBC Working Group on *Heliothis*?)
IX. Protocol for Deposition of Voucher Specimens
X. Identification of Computerized Databases that Require or Would Be Enhanced by Biosystematic Expertise.

Relationship with IACBSE

The Work Group Leader(s) will be designated by the Convenor with the advice of the IACBSE Executive Group. The Work Group and Project Leader(s) will provide the Convenor and IACBSE Executive Group with requests for financial support, for technical assistance, and will provide an annual report of accomplishments.

The Project Leader(s) are especially encouraged to seek assistance from the IACBSE regional representatives in identifying project participants. The Work Group is expected to be an international, cooperative, *action* group and thus is encouraged to make use of the IACBSE structure to achieve its goals, but communication should not be cumbersome or delay the progress of the Work Group. It is intended that the organization and communication be adequate to ensure effective international cooperation and to be competitive in applications for support. The Work Group Leader(s) and/or Project Leaders will be expected to participate in a Symposium at the XVIIIth International Congress of Entomology (Vancouver, British Columbia, Canada, 1988) to report on the progress of the Group/Project.

The IACBSE regional representatives provide leadership in systematics in the respective regions. They communicate regional concerns, needs, and activities; initiate and recommend projects; and coordinate programs at the regional level (see attached list of members).

Funding

The IACBSE Executive Group desires to assist in obtaining funding and other support for the Work Group and will assist in communicating with national and international sources of funding for the Work Group.

Publication

The Work Group participants will arrange for the publication of the

results of their projects. A credit line to the IACBSE, as appropriate in the acknowledgments, will be appreciated.

Membership

The membership of the International Advisory Council for Biosystematic Services in Entomology (IACBSE) is listed here by zone and region.

Palearctic zone

Region 1, Eastern Europe and USSR

Eastern Europe: J. Papp (Dept. of Zoology, Hungarian Natural History Museum, Budapest, Hungary)

USSR: V.F. Zaitzev (Zoological Institute, Academy of Sciences, Leningrad, USSR)

Region 2, Western Europe

United Kingdom: K.M. Harris (Commonwealth Institute of Entomology, London, England)

Continental Europe: R. zur Strassen (Forschungsinstitut Senckenberg, Frankfurt, Federal Republic of Germany)

Region 3, Far East

Japan: Y. Hirashima (Entomological Laboratory, Faculty of Agriculture, Kyushu University, Hakozaki, Japan)

People's Republic of China: Wu Yan-ru (Institute of Zoology, Academia Sinica, Beijing, People's Republic of China)

Africa/Near East zone

Region 4, Near East

Israel: D. Rosen (Department of Entomology, Faculty of Agriculture, Hebrew University, Rehovot, Israel)

Egypt: M.A. Zaher (Acarology Division, Agricultural Zoology Department, Faculty of Agriculture, Cairo University, Giza, Egypt)

Region 5, Eastern Africa

Kenya: J.M. Ritchie (Entomology Section, National Museums of Kenya, Nairobi, Kenya)

Region 6, Western Africa

Nigeria: A. Akingbohungbe (Department of Plant Science, University of Ife, Ile-Ife, Nigeria)

Oriental zone

Region 7, Southeast Asia

India: T.N. Ananthakrishnan (Entomology Research Institute, Loyola College, Madras, India)

Philippines: L.C. Raros (Department of Entomology, Visayas State College of Agriculture, Leyte, Philippines)

Australian-Oceania zone

Region 8, Australia, New Zealand, and Oceania

New Zealand: J.C. Watt (Entomology Division, Division of Scientific and Industrial Research, Auckland, New Zealand)

Nearctic zone

Region 9, North America

Canada: I.M. Smith (Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada)
Mexico: P. Reyes-Castillo (Instituto de Ecologia, A.C., Mexico, D.F.)
USA: L. Knutson (Biosystematics and Beneficial Insects Institute, U.S. Department of Agriculture, Beltsville MD, 20705, U.S.A.)

Neotropical zone

Region 10, Central America

Costa Rica: L. Fernando Jiron (Universidad de Costa Rica, Ciudad Universitaria, Rodrigo Facio, San José, Costa Rica)

Region 11, South America

Brazil: N. Papavero (Museu Goeldi, Belém, Para, Brazil)
Southern S.A: R. Gonzalez (Faculty of Agronomy, University of Chile, Santiago, Chile)

Representative-at-large

IACBSE Chair: K.C. Kim (The Frost Entomological Museum, Department of Entomology, The Pennsylvania State University, University Park, PA 16802, USA.)

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I. Spiders

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APPENDIX 1. ASSESSMENT OF TAXONOMIC EXPERTISE AND COLLECTION RESOURCES FOR *HELIOTHIS* AND MAJOR GROUPS OF NATURAL ENEMIES

Systematists and Their Locations

It is important for both systematists and researchers in areas related to systematics to have access to specific, detailed information on the systematists themselves (especially who is working on what) and on the collection resources available. This kind of information is usually needed for a specific group in a specific area, for example, the tachinid parasites of *Heliothis* in Africa. Such current information is difficult to obtain for a diverse group of organisms. I have had the assistance of the specialists in the Systematic Entomology Laboratory and others in developing the following lists. It should be noted that very few of the systematists listed below work extensively on *Heliothis* or on their natural enemies, but their general areas of expertise include these groups. It is not intended that the list includes all specialists in a certain family, but only those who may be of assistance with regard to natural enemies of *Heliothis* and *Helicoverpa*. Complete addresses are not given below for retired systematists or those who we know, or expect, do not wish to make identifications.

It is always essential that requests for identification be communicated to the taxonomists *before* sending specimens for identification. I must emphasize that I have not communicated directly with all of the specialists listed, and thus I cannot vouch for their ability or willingness to accept material for identification.

I hope that this information will enhance communication between taxonomists and those who need their assistance, and that the information will help to highlight areas needing attention.

Directory of systematists

A. *Heliothis*

Dr. I.B.F. Common, Division of Entomology, CSIRO, G.P.O. Box 1700, Canberra, A.C.T. 2601, Australia (retired)

Dr. David Hardwick, Biosystematics Research Center, Agriculture Canada (retired)

Dr. J.D. Holloway, Commonwealth Institute of Entomology, 56 Queens Gate, London, SW7 5JR, United Kingdom

Mr. Marcus Matthews, Dept. Entomology, British Museum (NH), Cromwell Road, London, SW7 5BD, United Kingdom (Cladistic analysis of Heliothinae).

Dr. Robert W. Poole, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington, D.C. 20560, USA

Mr. S.M. Maragal, Department of Entomology, University of Agricultural Sciences, Bangalore, India (Ph.D. research on biotypes of *H. armigera* and *H. assulta* in Karnataka by cross-mating studies, and economic loss on sunflower (with Prof. ChannaBasavanna).

Dr. Ebbe Nielsen, CSIRO Division of Entomology, GPO Box 1700, Canberra, ACT 2601, Australia (Taxonomy of *Heliothis* in Australia).

Mr. R.K. Siddiqui, Commonwealth Institute of Biological Control, Pakistan Station, Rawalpindi, Pakistan. (Survey of morphology of male and female genitalia of *Heliothis* in Pakistan, with cross-mating studies.)

B. Tachinidae

Dr. Paul H. Arnaud, Jr., Dept. of Entomology, California Academy of Science, Golden Gate Park, San Francisco, California 94118, USA

Dr. B.K. Cantrell, Entomology Branch, Dept. of Primary Industries, Meiers Road, Indooroopilly, Queensland 4068, Australia

Dr. Chao Chien-Ming, Institute of Zoology, Academia Sinica, Beijing, People's Republic of China

Dr. Raul Cortés, Facultad de Agronomia, Universidad de Chile, Casilla 1004, Santiago, Chile

Dr. Roger W. Crosskey, Dept. Entomology, British Museum (N.H.), Cromwell Road, London, SW7 5BD, United Kingdom.

Dr. J. Henrique Guimaraes, Inst. de Ciencias Biomedicas II, Universidade de Sao Paulo, Caixa Postal 4365, 00508—Sao Paulo, SP, Brazil

Dr. K.M. Harris, Commonwealth Institute of Entomology, 56 Queens Gate, London, SWT 5JR, United Kingdom

Dr. Benno Herting, Staatliches Museum für Naturkunde, Schloss Rosenstein, 7000 Stuttgart 1, Federal Republic of Germany

Dr. L.P. Mesnil, Switzerland (retired)

Dr. Vera Richter, Zoological Institute, Academy of Sciences, Leningrad, V-164, USSR

Dr. Curtis W. Sabrosky, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington, DC 20560, USA (retired)

Dr. H. Shima, Biological Laboratory, College of General Education, Kyushu University 01, Ropponmatsu, Fukuoka 810, Japan

Dr. D.M. Wood, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Ontario, K1A OC6, Canada

Dr. Norman E. Woodley, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington, D.C. 20560, USA

C. Braconidae

Mr. Jia-Hua Chen, Institute of Biological Control, Fujian Agricultural College, Fuzhou, Fujian Prov., People's Republic of China

Dr. Thomas Huddleston, Dept. Entomology, British Museum (NH), Cromwell Road, London, SW7 5BD, United Kingdom

Dr. Paul M. Marsh, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington DC 20560, USA

Dr. W.R.M. Mason, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Ontario, K1A OC6, Canada

Dr. Jeno Papp, Hungarian Natural History Museum, Baross utca 13, Budapest, Hungary

Dr. M.J. Sharkey, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Ontario, K1A OC6, Canada

Dr. Cornelius van Achterberg, Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, The Netherlands (identification of Old World species)

D. Chalcidoidea

There are over 200 persons listed as chalcid specialists for distribution of the specialty newsletter "CHALCID FORUM." The taxonomists listed below are primarily those known to be willing to assist in providing identifications.

Dr. Z. Bouček, Commonwealth Institute of Entomology, 56 Queens Gate, London SW7 5JR, United Kingdom

Dr. B.D. Burks, USA (retired)

Dr. E.C. Dahms, Queensland Museum, Gregory Terrace, Fortitude Valley, Brisbane, Australia 4006

Dr. G.A.P. Gibson, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Ontario, K1A OC6, Canada

Dr. L. DeSantis, Museo de la Plata, Paseo del Bosque, 1900 La Plata, Republica Argentina

Mr. Liao Ding-Shi, Institute of Zoology, Department of Insect Taxonomy and Faunology, Academia Sinica, Beijing, People's Republic of China

Dr. E.E. Grissell, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington DC 20560, USA

Dr. M. Hayat, Department of Zoology, Aligarh Muslim University, Aligarh 202001, U.P., India

Dr. Ian D. Naumann, CSIRO, Division of Entomology, P.O. Box 1700, Canberra City, ACT 2601, Australia

Dr. G.L. Prinsloo, Plant Protection Research Institute, Dept. Agric. and Technical Services, Private Bag X134, Pretoria, South Africa

Dr. M.E. Schauff, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington DC 20560, USA

Dr. C.M. Yoshimoto, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Ontario, K1A OC6, Canada

E. Trichogrammatidae

Dr. Mary Carver, University of Adelaide, Waite Agricultural Research Institute, South Australia 5064

Dr. S.L. de la Torre, Dpto. de Zoologia, Universidad de la Habana, Cuba

Dr. Yoshimi Hirose, Institute of Biological Control, Kyushu University, Fukuoka 812, Japan

Dr. A.C.F. Hung, Beneficial Insects Laboratory, Agricultural Research Service, USDA, Beltsville, MD 20705, USA

Dr. H. Nagaraja, Commonwealth Institute of Biological Control, Indian Station, Bangalore 560 006, India (Senior Entomologist, Biological Control Dept., ACA C11, c/o United Coconut Planters Bank, Magsaysay Ave., Davao City, Philippines)

Dr. Sudha Nagarkatti, 11130 Blue Heron Drive, Pineville, NC 28134, USA

Mr. K.S. Lin, Department of Applied Zoology, Taiwan Agricultural Research Institute, Wufeng, Taichung Hsien, Taiwan 431, Republic of China

Dr. Pang Xiong-fei, South China Agricultural University, Guangzhou, Guangdong, People's Republic of China

Dr. John D. Pinto, Department of Entomology, University of California, Riverside, CA 92521, USA

Dr. P. Pintureau, INRA, Station de Zoologie et de Lutte Biologique, 37, Bd. du Cap, 06602 Antibes, France

Dr. A.P. Sorokina, All-Union Research Institute for Plant Protection, Pushkin, USSR

Dr. B.R. Subba Rao, Commonwealth Institute of Entomology, 56 Queens Gate, London, SW7 5JR, United Kingdom

Dr. E.S. Sugonyaev, Zoological Institute, Academy of Sciences, Leningrad, 199164, USSR

Dr. G. Viggiani, Istituto di Entomologia Agraria, Universita di Napoli, Portici, Italy

Dr. J. Voegele, INRA, Station de Zoologie et de Lutte Biologique, 37, Bd. du Cap, 06602 Antibes, France

F. Ichneumonidae

Dr. J.R. Baron, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Ontario, K1A OC6, Canada

Dr. Robert W. Carlson, Systematic Entomology Laboratory, Biosystematics and Beneficial Insects Institute, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington DC 20560, USA.

Dr. Sui-Chen Chiu, Taiwan Agricultural Research Institute, Taipei, Republic of China

Dr. Ian Gauld, Dept. of Entomology, British Museum (NH), Cromwell Road, London, SW7 5BD, United Kingdom

Dr. V.K. and **Mrs. S. Gupta,** American Entomological Institute, c/o Dept. of Entomology, University of Florida, Gainesville, FL 32611, USA

Dr. Junhua He, Dept. of Plant Protection, Zhejiang Agricultural University, Hangzhou, Zhejiang Prov., People's Republic of China

Dr. K. Kusigemati, Kagoshima, Japan

Dr. J.W. Lee, Dept. of Biology, Korea University, Seoul, Korea

Dr. H.K. Townes, American Entomological Institute, 3005 SW 56th Avenue, Gainesville, FL 32611, USA

Ms. Sufang Wang, Dept. of Insect Taxonomy and Faunology, Academia Sinica, Beijing, People's Republic of China

Dr. Qui-Ti You, Institute of Agriculture, Nantung, Jiangsu Province, People's Republic of China

Dr. Shi-Jin You, Institute of Agriculture, Nantung, Jiangsu Province, People's Republic of China

Dr. XiuFu Zhao, Fujian Agricultural College, Fuzhou, Fujian Province, People's Republic of China

G. Heteroptera

Anthocoridae:

Dr. J. Carayon, Museum National Histoire Naturelle, Paris (retired)

Mr. T.J. Henry, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum of Natural History, Washington DC 20560, USA

Dr. L.A. Kelton, Biosystematics Research Institute, Agriculture Canada, Ottawa (retired)

Dr. J. Pericart, 10 Rue Habert, F-77130, Montereau, France

Geocorinae:

Dr. J.A. Slater, Biological Sciences Group, University of Connecticut, Storrs, CT 06268, USA

Dr. M.L. Sweet, Department of Biology, Texas A&M University, College Station, Texas 77843, USA

Miridae:

Dr. J.C.M. Carvalho, Museu Nacional, Rio de Janeiro, Brasil (retired)

Mr. T.J. Henry, Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum of Natural History, Washington DC 20560, USA

Dr. L.A. Kelton, Biosystematics Research Institute, Agriculture Canada, Ottawa, Canada (retired)

Dr. I.M. Kerzhner, Zoological Institute, Academy of Sciences, Leningrad, USSR

Dr. J.C. Schaffner, Department of Entomology, Texas A&M University, College Station, Texas 77843, USA

Dr. R.T. Schuh, Department of Entomology, American Museum of Natural History, Central Park West at 79th St., New York NY 10024, USA

Dr. G.M. Stonedahl, Department of Entomology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA

Nabidae:

Dr. I.M. Kerzhner, Academy of Sciences, Zoological Institute, Leningrad, USSR

Dr. J.D. Lattin, Department of Entomology, Oregon State University, Corvallis OR 97331, USA

H. Predatory Wasps

Eumenidae:

Dr. J. Carpenter, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

Mr. J.M. Cumming, Department of Entomology, University of Alberta, Edmonton, Canada T6G 2E3

Dr. J. Gusenleitner, Landw.-chemische, Bundesversuchsanstalt Linz, George Wieningerstrasse 8, A4025 Linz/Donau, Austria

Dr. J. Kojima, Department of Natural History, Faculty of Science, Tokyo Metropolitan University, Fukazawa, Setagaya, Tokyo 158, Japan

Dr. A.S. Menke, Systematic Entomology Laboratory, Agricultural

Research Service, USDA, c/o U.S. National Museum, Washington DC 20560, USA

Dr. **A.G. Soika,** Museo Civico di Storia Naturale, Santa Croce 1730, Venice, Italy

Dr. **J. van der Vecht,** "Andrena," Burg, Vermeerlaan 4, 3881 GZ Putten (Gld.), The Netherlands

Dr. **A. Willink,** Fac. de Ciencias Naturales, Instituto Miguel Lillo, Miguel Lillo 205, 4000 Tucuman, Argentina

Vespidae:

Dr. **M.E. Archer,** Department of Biology, College of Ripon and York St. John, York YO3 7EX, United Kingdom

Dr. **R. Eck,** Staatliches Museum für Tierkunde Dresden, Augustusstrasse 2, DDR-8010 Dresden, German Democratic Republic

Dr. **A.S. Menke,** Systematic Entomology Laboratory, Agricultural Research Service, USDA, c/o U.S. National Museum, Washington DC 20560, USA

Dr. **Lee Tie Sheng**

Mr. **R. Snelling,** Department of Entomology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles CA 90007, USA

Mr. **Seiki Yamane,** Department of Biology, Kagoshima University, Korimoto, Kagoshima, 890 Japan

Dr. **Soichi Yamane,** Biological Laboratory, Faculty of Education, Ibaraki University, Mito, 310 Japan

I. Chrysopidae

Dr. **P.A. Adams,** Department of Biological Sciences, California State University, Fullerton CA 92634, USA

Dr. **H. Aspöck,** Hygenie-Institut der Universität, Kinderspitalgasse 15, A-1095, Wien, Austria

Dr. **P.C. Barnard,** Department of Entomology, British Museum (Natural History), Cromwell Rd., London, SW7 5BD, United Kingdom

Dr. **T.R. New,** Department of Zoology, LaTrobe University, Bundoora, Victoria 3083, Australia

Dr. **Peter Ohm,** Zoologisches Museum, Hegewischstrasse 3, D-2300 Kiel 7, Federal Republic of Germany

J. Spiders

(The following information was provided by Dr. Jonathan A. Coddington, Dept. Entomology, Smithsonian Institution. Dr. Coddington noted (*in litt.*) that, "It is difficult to provide a cogent list of taxonomists because spiders are such generalist predators. [The taxonomists listed generally] focus on the fauna of their country, or a wider area."

Dr. Allen Brady, Department of Biology, Hope College, Holland, MI 49423, USA

Dr. Jonathan Coddington, Department of Entomology, Smithsonian Institution, Washington, DC 20560, USA

Dr. P.M.C. Croeser, Acarology Dept., Natal Museum, Loopstraat 237, Pietermaritzburg 3201 Natal, Republic of South Africa

Dr. Anna Timotheo da Costa, Museu Nacional, Quinta da Boa Vista, Rio de Janeiro (GB), Brazil

Dr. Valerie T. Davies, Queensland Museum, Gregory Terrace, Fortitude Valley, Queensland 4006, Australia

Dr. Charles D. Dondale, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario K1A OC6, Canada

Dr. G.B. Edwards, Division of Plant Industry, P.O. Box 1269, Gainesville, Florida 32602, USA

Dr. R.R. Forster, Otago Museum, Great Kings Road, Dunedin, New Zealand

Dr. Maria Elena Galiano, Mus. Argent. Ciencias Naturales, Avda. Angel Calardo 470, Casilla de Correo 10, Sucursal 5, 1405 Buenos Aires, Argentina

Dr. Willis J. Gertsch, P.O. Box 157, Portal, AZ 85632, USA

Mr. Michael R. Gray, Arach. Dept., The Australian Museum, 6–8 College Street, P.O. Box A285 Sydney South, N.S.W. 2000, Australia

Dr. Norman Horner, 3400 Taft, Midwestern State University, Wichita Falls, Texas 76308, USA

Dr. R. Jocque, Musee Royal de l'Afrique Central, B-1980 Tervuren, Belgium

John A. Kochalka, Inventario Biologico Nacional, Servicio Forestal Nacional, Edificio Patria, 6 piso, Tacuary 443, Asuncion, Paraguay

Dr. Pekka Lehtinen, Zoological Institute, University of Turku, Turku, Finland

Dr. H.W. Levi, Dept. Invertebrates, Museum of Comparative Zoology, Harvard University, Cambridge, MA 01238, USA

Dr. Gershom Levy, Dept. Zoology; Hebrew Univ. of Jerusalem, Jerusalem, Israel

E.A. Maury, Arachnologia, Mus. Argent. Ciencias Naturales, Avda. Angel Calardo 470, Casilla de Correo 10, Sucursal 5, Buenos Aires, Argentina

Dr. Hirotsugu Ono, Section of Entomology, National Science Museum, 3-23-1 Hyakunin–cho, Shinjuku-ku, Tokyo 160, Japan

Kap Yong Paik, Teachers College, Kyungpook University, Taegu, Korea

Dr. B.H. Patel, Department of Zoology, SIR P.P. Institute of Science Bhavnagar, 364002, Gujarat, India

Mr. Louis E. Peña, Casilla 2974, Santiago, Chile

Dr. Norman I. Platnick, Department of Entomology, American Museum of Natural History, Central Park West at 79th, New York NY 10024, USA

Dr. Robert J. Raven, Queensland Museum, Gregory Terrace, Fortitude Valley, Queensland 4006, Australia

Dr. Da-Xiang Song, Institute of Zoology, Academia Sinica, 7 Zhong-guancun, Haitien, Beijing (53), People's Republic of China

Dr. Seisho Suzuki, The Hiroshima Arachnological Laboratory, 17-2 Nishihakushima-cho, Hiroshima-shi 730, Japan

Dr. B.J. Tikader, Director, Zoological Survey of India, 34 Chittaranjan Avenue, Calcutta 700012, India

Dr. Carlos E. Valerio, Departamento de Biologia, Universidad de Costa Rica, Ciudad Universitaria, San Jose, Costa Rica

Dr. V.R.D. von Eickstedt, Secão de Atropodos Peconhentos, Instituto Butantan, Caixa Postal 65, São Paulo, Brasil

Mr. F.R. Wanless, Division of Arachnids & Myriapods, British Museum, Natural History; Cromwell Road, London SW7 5BD, UK

Dr. Takeo Yaginuma, Biological Laboratory, Ohtemon-Gakuin University, 2-1-15 Nishi-ai, Ibaraki, Osaka 567, Japan

Mr. Hajime Yoshida, 2-7-18 Kagota, Yamagata 990, Japan

Dr. Makoto Yoshikura, 151 Takahira, Shimizu-machi, Kumamoto-shi 860, Japan

Specialists by Taxon and Region

A. *Heliothis*

> AFRICA: Matthews
> AUSTRALIA-NEW ZEALAND: Common, Nielsen
> SOUTHERN ASIA: none
> CHINA: none
> INDIA-PAKISTAN: none
> NORTH AMERICA: Hardwick
> SOUTH AMERICA: none

B. Tachinidae

Mesnil, the leading world authority who has worked intensively on the Palearctic, Oriental and Afrotropical faunas, is retired. Herting is a specialist on the Palearctic fauna and probably handles necessary identifications. Richter publishes to some extent on the fauna of the USSR. Shima is an excellent young worker, with experience chiefly in the Eastern Palearctic. With Crosskey at the British Museum no longer actively working on Tachinidae, identifications for African and Oriental material will be difficult. Harris provides identifications at the Commonwealth Institute of Entomology.

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There is expertise in the New World, with Wood, Arnaud, Woodley, and Guimaraes still active. Sabrosky is retired. Cortés has worked primarily on the Chilean fauna.

AFRICA: Crosskey is the best specialist but has practically withdrawn from providing identifications in Tachinidae and is now concentrating on Simuliidae.

AUSTRALIA-NEW ZEALAND: Cantrell has published a few papers and is preparing a manuscript for the Catalog of Australian and Oceanian Diptera.

SOUTHERN ASIA: Shima has studied Japanese fauna chiefly, but seems to be broadening his interests.

CHINA: Chao Chien-Ming is the leading worker on tachinids in China.

INDIA-PAKISTAN:

NORTH AMERICA: Sabrosky, retired. Wood is an excellent specialist. Woodley is just beginning study of the family. Arnaud conducts extensive field work.

SOUTH AMERICA: Guimaraes has done much with the family and has authored the South American catalog of Tachinidae. Cortés, near retirement, has published a number of papers, almost entirely on the Chilean fauna.

C. Braconidae

AFRICA: Huddleston is revising *Chelonus* for the Old World. Papp (identification).

AUSTRALIA-NEW ZEALAND: none

SOUTHERN ASIA: Huddleston, Papp.

CHINA: Chen (identification)

INDIA-PAKISTAN: Huddleston, Papp.

NORTH AMERICA: Marsh (identification; no plans for revisionary work), Mason, Sharkey

SOUTH AMERICA: none

D. Chalcidoidea

AFRICA: Bouček, Prinsloo

AUSTRALIA-NEW ZEALAND: Bouček, Dahms, Naumann

SOUTHERN ASIA: Bouček, Subba Rao

CHINA: Liao Ding-Shi

INDIA-PAKISTAN: Hayat, Subba Rao

NORTH AMERICA: Gibson, Grissell, Schauff, Yoshimoto

SOUTH AMERICA: DeSantis

E. Trichogrammatidae

AFRICA: Pintureau, Voegele

AUSTRALIA-NEW ZEALAND: Carver, Subba Rao
SOUTHERN ASIA: Lin, Nagaraja, Pang
CHINA: Hung, Lin, Pang
INDIA-PAKISTAN: Nagaraja, Subba Rao
NORTH AMERICA: Hung, Pinto
SOUTH AMERICA: Pinto, Torre

F. Ichneumonidae
AFRICA: Gauld
AUSTRALIA-NEW ZEALAND: Bain, Gauld
SOUTHERN ASIA: Gauld, S. Gupta, V.K. Gupta, Kusigemati
CHINA: Junhua He, Lee, Qui-Ti You, Shi-Jin You, Sufang Wang,
    Sui-Chen Chiu, Xiufu Zhao.
INDIA-PAKISTAN: S. Gupta and V.K. Gupta
NORTH AMERICA: Barron, Carlson, S. Gupta, V.K. Gupta, H.K.
    Townes.
SOUTH AMERICA: S. Gupta, V.K. Gupta, H.K. Townes.

G. Heteroptera—No specialists concentrating on natural enemies of
    Heliothis

H. Predatory Wasps—No specialists concentrating on natural enemies of
    Heliothis

I. Chrysopidae
AFRICA—Barnard
AUSTRALIA—New
SOUTHERN ASIA—None
CHINA—None
INDIA, PAKISTAN—None
NORTH AMERICA—Adams
SOUTH AMERICA—Adams

J. Coccinellidae—No specialists concentrating on natural enemies of
    Heliothis

K. Spiders—No specialists concentrating on natural enemies of *Heliothis*
AFRICA: Croeser
AUSTRALIA: Davies, Forster, Gray, Raven
SOUTHERN ASIA: Ono, Suzuki, Yaginuma, Yoshida, Yoshikura
CHINA: Paik, Da-Xiang Song
INDIA, PAKISTAN: Patel, Tikader
NORTH AMERICA: Brady, Coddington, Dondale, Edwards, Gertsch,
    Horner, Levi, Platnick

SOUTH AMERICA: Galiano, Kochalka, Maury, Peña, da Costa, Valerio, von Eickstedt

Collection Resources—Locations and Quality of Major Collections

Research collections will in general be a more important source of information on biology, hosts, etc., for parastic groups than for predaceous groups.

Directory of Collections

AEI—American Entomological Institute, c/o Dept. of Entomology, University of Florida, Gainesville FL 32611, USA

AMNH— American Museum of Natural History, Central Park West at 79th St, New York NY 10024, USA

ASB—Institute of Zoology, Dept. of Insect Taxonomy and Faunology, Academia Sinica, Beijing, People's Republic of China

BM(NH)—British Museum (Natural History), Dept. of Entomology, Cromwell Road, London, SW7 5BD, United Kingdom

CAS—California Academy of Science, Golden Gate Park, San Francisco, CA 94118, USA

CIBCI—Commonwealth Institute of Biological Control, Indian Station, Bangalore, India

CNC—Canadian National Collection, c/o Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Ontario, K1A OC6, Canada

CSIRO—Division of Entomology, Commonwealth Scientific and Industrial Research Organization, P.O. Box 1700, Canberra City, ACT 2601, Australia

DSIR—Department of Scientific and Industrial Research, Auckland, New Zealand

FAC—Fujian Agricultural College, Fuzhou, Fujian Province, People's Republic of China

IML—Instituto Miguel Lillo, Miguel Lillo 205, 4000 Tucuman, Argentina

IRSNB—Institut Royal des Science Naturelle de Belgique, Brussels, Belgium

IZACC—Instituto de Zoologia de la Academie de Ciencias de Cuba, Havana, Cuba

JAS—J.A. Slater Collection, University of Connecticut, Storrs CT 06268 USA

KK—K. Kusigemati, Kagoshine University, Japan

MACN—Museo Argentino de Ciencias Naturales (Bernardino Rivadavia), Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina

MAE—Department of Entomology, Ministry of Agriculture, Cairo, Egypt

MAKB—Museum Alexander Koenig, Bonn, Federal Republic of Germany

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge MA 02139, USA

MNB—Museu Nacional, Rio de Janeiro, Brasil

MNHNP—Museum National Histoire Naturelle, Paris

MLP—Museo de La Plata, Paseo del Bosque, 1900 La Plata, Argentina

MZU—Museu de Zoologia de Universidade de Sao Paulo, Caixa Postal 7172, Sao Paulo, Brasil

PPRI—Plant Protection Research Institute, Department of Agriculture and Technical Services, Private Bag X134, Pretoria, South Africa

QM—Queensland Museum, Gregory Terrace, Fortitude Valley, Brisbane, Australia 4006

TAM—Texas A&M University, College Station TX 77843, USA

TARIT—Taiwan Agricultural Research Institute, Taichung, Republic of China

TMP—Transvaal Museum, Pretoria, South Africa

UCB—University of California, Berkeley CA, USA

UCD—University of California, Davis CA, USA

UCR—University of California, Riverside CA, USA

UD—University of Delhi, Delhi, India

UFG—University of Florida, Gainesville FL, USA

USNM—United States National Museum, Smithsonian Institution, Washington DC 20560, USA

ZIL—Zoological Institute, Academy of Sciences, Leningrad, USSR

ZMHF—Zoological Museum, Division of Entomology, Helsinki, Finland

A. *Heliothis*

    AFRICA: BM(NH), most of the type material; MNHNP, TMP, USNM
    AUSTRALIA-NEW ZEALAND: BM(NH), CSIRO
    SOUTHERN ASIA: BM(NH)
    CHINA: MAKB
    INDIA-PAKISTAN: BM(NH)
    NORTH AMERICA: AMNH, CNC, LACM, USNM
    SOUTH AMERICA: USNM

B. Tachinidae

    AFRICA: Mesnil Collection at CNC, BM(NH)
    AUSTRALIA-NEW ZEALAND: CSIRO—Quality fairly good in the named collections, although uneven. Scattered collections at AMNH (Curran types), BM(NH), CAS, Mesnil Collection in CNC, DSIR.

SOUTHERN ASIA: BM(NH), CNC, CSIRO
CHINA: BM(NH), CNC, CSIRO
INDIA-PAKISTAN: BM(NH), CNC, CSIRO
NORTH AMERICA: Arnaud private collection rich in well-mounted material. CNC and USNM. (Townsend types in U.S. National Museum especially important.)
SOUTH AMERICA: BM(NH) (*Biologia* types), CNC, UMSP, USNM (Townsend types)

C. Braconidae

AFRICA:BM(NH), MAE?
AUSTRALIA-NEW ZEALAND: ?
SOUTHERN ASIA: ?
CHINA: Possibly good collections at ASB. Probably good collections at FAC.
INDIA-PAKISTAN: ?
NORTH AMERICA: CNC; good collection of reared specimens and types of Cushman, Ashmead, and Viereck at USNM
SOUTH AMERICA: Some material from Argentina in USNM

D. Chalcidoidea

AFRICA: PPRI?
AUSTRALIA-NEW ZEALAND: CSIRO?, QM?
SOUTHERN ASIA: BM(NH)
CHINA: AS—fair
INDIA-PAKISTAN: BM(NH)
NORTH AMERICA: CNC and UCR—good; USNM—very good
SOUTH AMERICA: MLP?

E. Trichogrammatidae

AFRICA: MNHNP
AUSTRALIA-NEW ZEALAND: BM(NH), CSIRO
SOUTHERN ASIA: ASB, CIBCI, TARIT, USNM
CHINA: ASB, TARIT, USNM
INDIA-PAKISTAN: BM(NH), CIBCI, USNM
NORTH AMERICA: UCR, USNM
SOUTH AMERICA: IZACC, UCR, USNM

F. Ichneumonidae

AFRICA: AEI, BM(NH), IRSNB?
AUSTRALIA-NEW ZEALAND: AEI, BM(NH), CSIRO
SOUTHERN ASIA: AEI, KU
CHINA: ASB, BM(NH), TARIT

INDIA-PAKISTAN: AEI, BM(NH), CNC, UD, USNM

NORTH AMERICA: Reared material primarily at CNC, UCR, and USNM; greatest concentration of material (mostly unreared) in AEI and UFG.

SOUTH AMERICA: AIE, BM(NH), CNC, UFG, IML, MACN, USNM

G. Heteroptera

Anthocoridae: BM(NH), CNC, MNHNP, ZMHF

Geocorinae: BM(NH), JAS, TAM, USNM

Miridae: AMNH, BM(NH), CAS, CNC, MNB, MNHNP, TAM, USNM, ZIL, ZMHF

Nabidae: BM(NH), USNM, ZIL

H. Predatory wasps

BM(NH), CAS, MCZ, UCB, UCD, USNM

I. Chrysopidae

BM(NH), CNC, CSIRO, MCZ, USNM

J. Coccinellidae

BM(NH), CNC, CSIRO, MCZ, USNM

A General Synopsis of the Systematics of *Heliothis* and *Helicoverpa*

*Robert W. Poole**

ABSTRACT

A general synopsis of the current state of the systematics of *Heliothis*, *Helicoverpa*, and the rest of the subfamily Heliothinae is given. The current groupings in the corn earworm complex, the genus *Helicoverpa*, and their known distributions and pest status are discussed. It is recommended that the genus *Helicoverpa* be used for the corn earworm complex because of the great dissimilarity between these species and the rest of the species currently placed in *Heliothis*. It is also recommended that the original spelling of the specific name be used rather than trying to conform to the current rule of the specific name agreeing in number and gender with the generic name. The genus *Heliothis* is then discussed followed by short presentations on related genera of some size but little economic importance.

The scientific nomenclature of "Heliothis" moths has been a subject of controversy and a matter of confusion for many years. There are three practical problems afflicting the systematic study of the species included in "Heliothis" in the broadest sense of that term. These three problems are:

1. Should the members of the corn earworm complex (e.g. *armigera* and *zea*) be separated from *Heliothis* in their own genus *Helicoverpa*?

2. What is the correct ending for each of the specific names of the species included in *Heliothis* and *Helicoverpa*?

3. What is the correct spelling of the subfamily name?

The purpose of this manuscript is to try and resolve these three questions and to give a general overview of the systematics and phylogeny of the subfamily Heliothinae of the family Noctuidae and in particular the genera *Heliothis* and *Helicoverpa*. The first question everyone will have, I

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NOTE: Submitted paper, but not presented at Workshop.

am sure, is what is *Helicoverpa*. A little historical background is in order. Until fairly recently the members of the corn earworm complex (including for example *H. zea* and *H. armigera*) were included in the genus *Heliothis* along with the type species of *Heliothis, Phalaena dipsacea* Linnaeus, a species now called *Heliothis viriplaca* (Hufnagel), as well as many other species including the four described species of the tobacco budworm complex (e.g. *virescens* and *subflexa*). The inclusion of the members of the corn earworm complex in *Heliothis* was due almost entirely to the superficial similarity of *armigera, zea,* and their allies to the type-species of *Heliothis, H. viriplaca,* and not to any close morphological similarity. In 1965 Hardwick revised the members of the corn earworm complex (Hardwick, 1965). One of the conclusions reached in this important and thorough work is that the members of the corn earworm complex were very different from the other species in the genus *Heliothis* and apparently not at all closely related to them phylogenetically. Hardwick, therefore, proposed the generic name *Helicoverpa* for the species of the corn earworm complex.

His use of the generic name *Helicoverpa* for the species in the corn earworm complex was accepted by some taxonomists, but not by others. In the economic literature *Heliothis* is still being used for *zea, armigera,* and their allies. The decision to retain *armigera* and *zea* in *Heliothis* was made by most scientists largely to avoid confusion among non-taxonomists by changing the generic names of this tremendously important group of insects. This was the opinion of my predecessor at the Systematic Entomology Laboratory and my own decision until fairly recently. However a number of reasons have compelled me to change my mind and to decide that the members of the corn earworm complex should be treated as a genus separate from *Heliothis*. This decision was made after careful analysis and consultation with non-taxonomic workers on the corn earworm and tobacco budworm.

1. Scientifically, Hardwick is correct. The species of *Helicoverpa* are morphologically distinct from all other species in the Heliothinae. The species possess two important unique derived (apomorphic in the terminology of systematics) characteristics found nowhere else in the subfamily. Also the larvae of *Helicoverpa* are very distinct from the larvae of *Heliothis*. One of the fundamental principles of systematics is that generic groupings can be defined only on the basis of shared derived characters. These characters are discussed in the section on *Helicoverpa*. Phylogenetically the genus *Helicoverpa* is probably even less related to the true species of *Heliothis* than proposed by Hardwick.

2. We risk the danger of making unwarranted comparisons or analogies between biological characteristics of the corn earworm complex and the species in *Heliothis*, particularly the tobacco budworm complex.

Because these two groups of species are so distantly related, it would be extremely dangerous to assume that anything true of *Heliothis virescens*, for example, could be expected to be true of *Helicoverpa zea*. The use of two different generic names will tend to emphasize the distinctness of these two important groups and help avoid misunderstandings of their relative relatedness to each other.

3. Discussions with several non-taxonomists involved with *Heliothis* and *Helicoverpa* have convinced me that the introduction of the generic name *Helicoverpa* for the members of the corn earworm complex will not be as confusing to "*Heliothis*" (in the old sense) workers as I had originally thought.

SPECIES NAME ENDINGS

The international rules of zoological nomenclature stipulate that the ending of a species group name must agree in number and gender with the generic name. The current confusion over the correct spellings for the endings of the species group names in *Heliothis* and *Helicoverpa* can be traced to this antiquated rule. Historically the generic name *Heliothis* has been treated as feminine, but more recently some have claimed it is masculine and have changed the species endings to reflect a masculine gender for *Heliothis*. It is my contention and the contention of many others that for the purposes of stability, communication between workers, and electronic retrieval of papers and data, the only consistent and stable ending for a species is the ending originally given to it by the person who first described the species. In a catalogue I have just completed of the Noctuidae of the World, this rule has been applied consistently. All of the species endings employed in this paper are the original spellings and I recommend that this be the standard for workers on *Heliothis* in the broad sense. In every case that I am aware of application of this rule results in use of the ending originally familiar to non-systematic workers on the group. For species of *Heliothis* not included in this paper, a complete catalogue of the genus is available upon request from the author.

The conversion from a feminine to masculine interpretation of the gender of *Heliothis* also affects the spelling of the subfamily name; however, the traditional spelling of the subfamily name is Heliothinae. I recommend that workers use this spelling.

PHYLOGENY OF THE HELIOTHINAE

The Heliothinae are fairly easy to recognize as a group by superficial appearance, but they are difficult to define morphologically. This difficulty is largely due to a combination of either primitive characters, i.e., characters shared with other primitive noctuid groups, and simplification

of morphological structures. I know of no single shared derived character to define the group as a whole. However I have doubt that the subfamily is a natural monophyletic unit. Incidentally this tendency towards simplification in morphological structure tends to make the systematics of the subfamily difficult. Perhaps the best character defining the subfamily is the habit of the larvae of feeding on the flowers or fruits of herbaceous plants. Although feeders on flowers and fruits are found in other groups of the Noctuidae, it is one of the essential characteristics of apparently all species in the subfamily Heliothinae. The nearest ancestral group of the Heliothinae is not known for certain, although several groups have been proposed as the sister (most closely related) group of the Heliothinae by different workers.

The North American genera of the Heliothinae have been studied by Hardwick (1970) and Figure 1 represents a hypothetical phylogeny for the subfamily for the North American genera only. The phylogeny (evolutionary history) is hypothetical in the sense that it represents Hardwick's best estimate of the actual evolutionary history of the subfamily, based on the characters he was able to examine. Although this phylogenetics study does not include the genera of Heliothinae not found in North America, this is probably not a significant weakness of the study because of the strong representation of the genera in North America, where the subfamily Heliothinae is best developed.

In Hardwick's phylogeny, two major groups are defined. In the first group (the left side of the figure) spines on the prothoracic tibiae have been lost. This group contains generally small genera with often rare species, most occurring in the western USA. The only exception is genus *Pyrrhia*. Although this genus contains only a few species, some species are of occasional economic importance in the USA and Europe.

The right side of the phylogeny represents those genera with spines on the prothoracic tibiae. Among the genera in this group are *Heliothis* and *Helicoverpa*. Among the remaining genera, *Schinia* is the most noteworthy. This genus is strongly developed in North America, where there are over 120 species; approximately 10 to 15 more are found in eastern Europe and Central Asia. All of the species of *Schinia* feed on the flowers or seeds of herbaceous plants, particularly the Compositae. None of the species, however, is known to be of any economic importance, although a few species in eastern North America feed on ragweed. *Helicoverpa* and *Heliothis* are treated below.

Among the Old World genera not treated in Hardwick's phylogeny is *Masalia*. This genus contains about 40 species, all of which occur either in Africa, India, or western China, though none is of any known economic importance. Generally, the species of *Masalia* are a rather pretty pink and yellow. The genus was revised by Seymour (1972). A second respectably
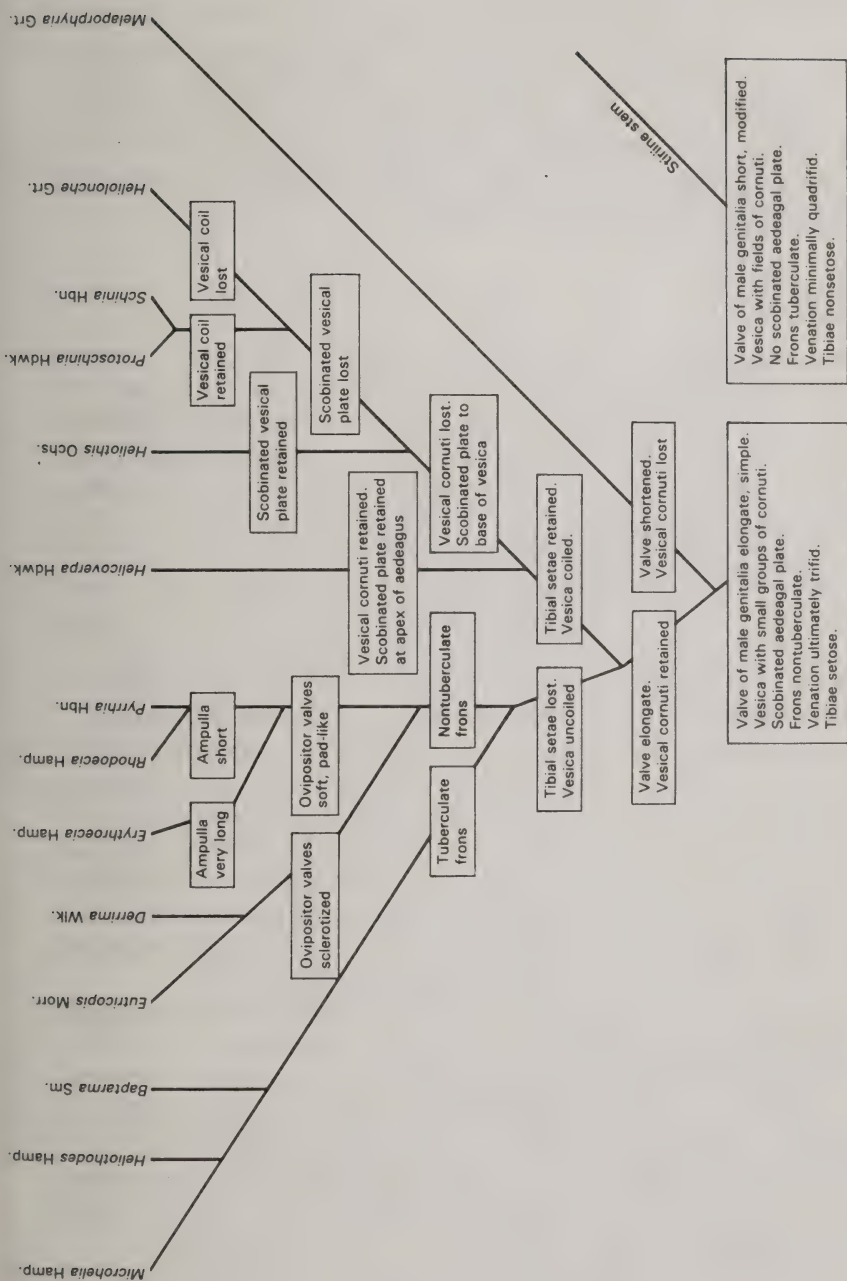
Figure 1. Possible phylogenetic derivation of genera of the Heliothidinae.

large genus is *Canthylidia*, which is almost exclusively Australian, occurring primarily in the drier regions of the country. There are about 50 species in the genus, but the systematics of the genus are poorly known. Finally, the genus *Raghuva* is almost entirely African with a few species in India. *Raghuva* is defined by a strange modification of the forewing in males. The genus may be related to *Heliothis paradoxus* of the USA and Mexico. In any case, the evolutionary affinities of all three of these Old World genera are undoubtedly with *Heliothis*.

HELICOVERPA

As already mentioned, the genus *Helicoverpa* is a very distinct element within the Heliothinae and very distinct from the species of *Heliothis*. In particular, the genus *Helicoverpa* (the corn earworm complex) is defined by: (1) the corkscrew or coiled vesica of the male aedeagus (penis) with strong spines (also called cornuti) along the rotational axis of the vesica and (2) a row of specialized seta-like scales along the ventral margin of the prothoracic femur. For example, compare the male genitalia of *Heliothis virescens* and *Heliothis viriplaca* in Figure 2 with the male genitalia of *Helicoverpa zea* and *H. armigera* in Figures 3 and 4. Neither of these characteristics is found in any other group of the Heliothinae, or for that matter the Noctuidae as a whole. *Helicoverpa* (the corn earworm complex) was revised by Hardwick (1965). Hardwick divided the genus into 17 species relegated to five species complexes. The 17 species are closely related and superficially very similar in appearance. For example, I am unable to separate *Helicoverpa zea* and *H. armigera* on the basis of external appearance. Authoritative identifications can be made only on the basis of an examination of the male or female genitalia. Also, special techniques are involved in the dissection of the male genitalia. The male and female genitalia of the two most important species of *Helicoverpa* are illustrated in Figures 3 and 4. The five species complexes are:

    1. The *punctigera* group: this contains the single species *punctigera* (Wallengren) from Australia. It is of economic importance.

    2. The *gelotopoen* group: this group contains four species from southern South America; *H. bracteae* Hardwick (Paraguay, Argentina, Peru—no known economic importance), *H. titicacae* Hardwick (Peru—no known economic importance), *H. gelotopoen* (Dyar) (Chile, Argentina, Uruguay, Brazil, Paraguay—minor economic importance), and *H. atacamae* Hardwick (Chile, Peru—no known economic importance).

    3. The *hawaiiensis* group contains two species, *H. hawaiiensis* and *H. pallida*, both endemic to the Hawaiian Islands and neither of known economic importance.
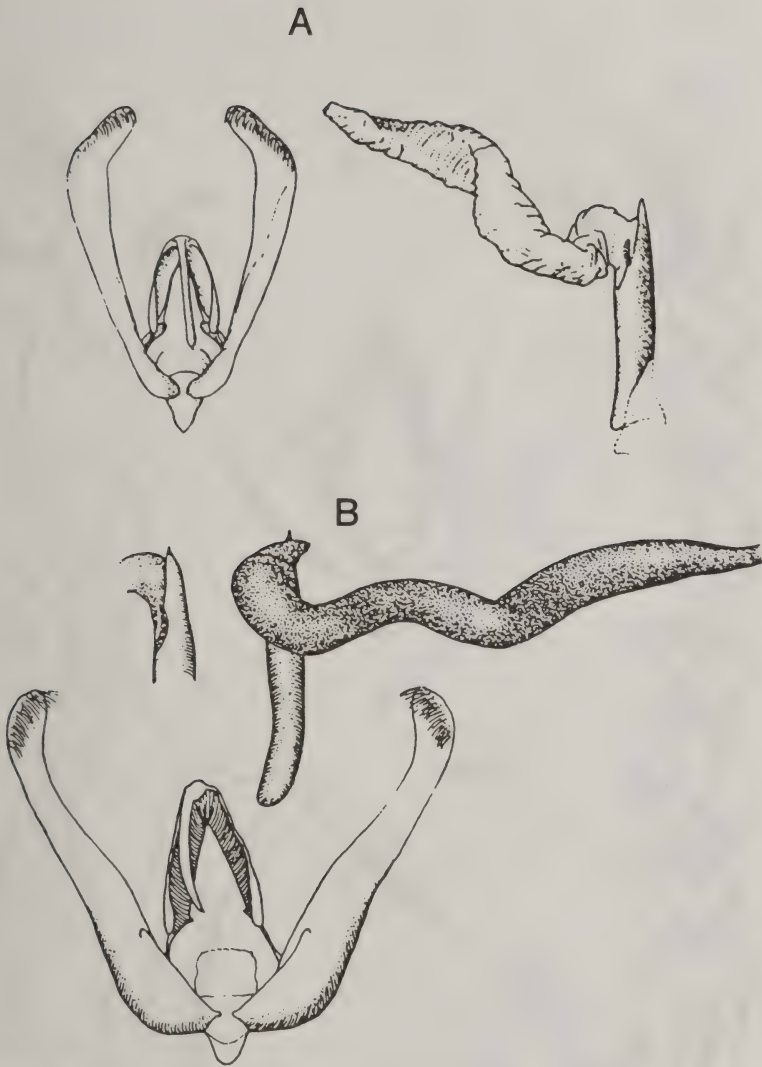
Figure 2. The male genitalia of: A. *Heliothis viriplaca* (Hufnagel) and B. *Heliothis virescens* (Fabricius).

4. The *armigera* complex contains two species, *H. armigera* (Hübner) (entire eastern tropical and subtropical hemisphere—great economic importance), and *H. helenae* Hardwick (St. Helena Island—no known economic importance).

5. The *zea* complex contains eight species: *H. zea* (Boddie) (entire western hemisphere except the far north and far south—great economic importance), *H. confusa* Hardwick (Hawaii—no known economic importance), *H. minuta* Hardwick (Hawaii—no known economic importance),
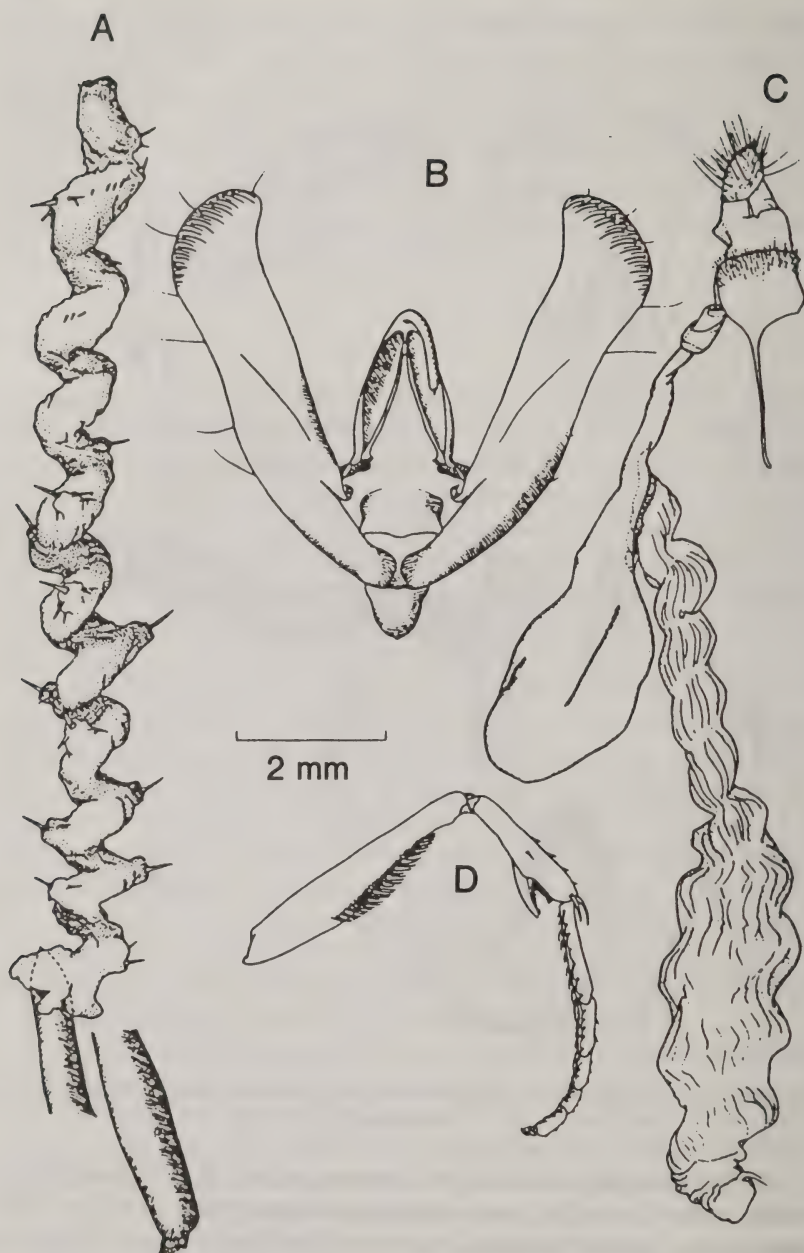
Figure 3. *Helicoverpa zea* (Boddie): A, B—male genitalia; C—female genitalia; D—right foreleg.
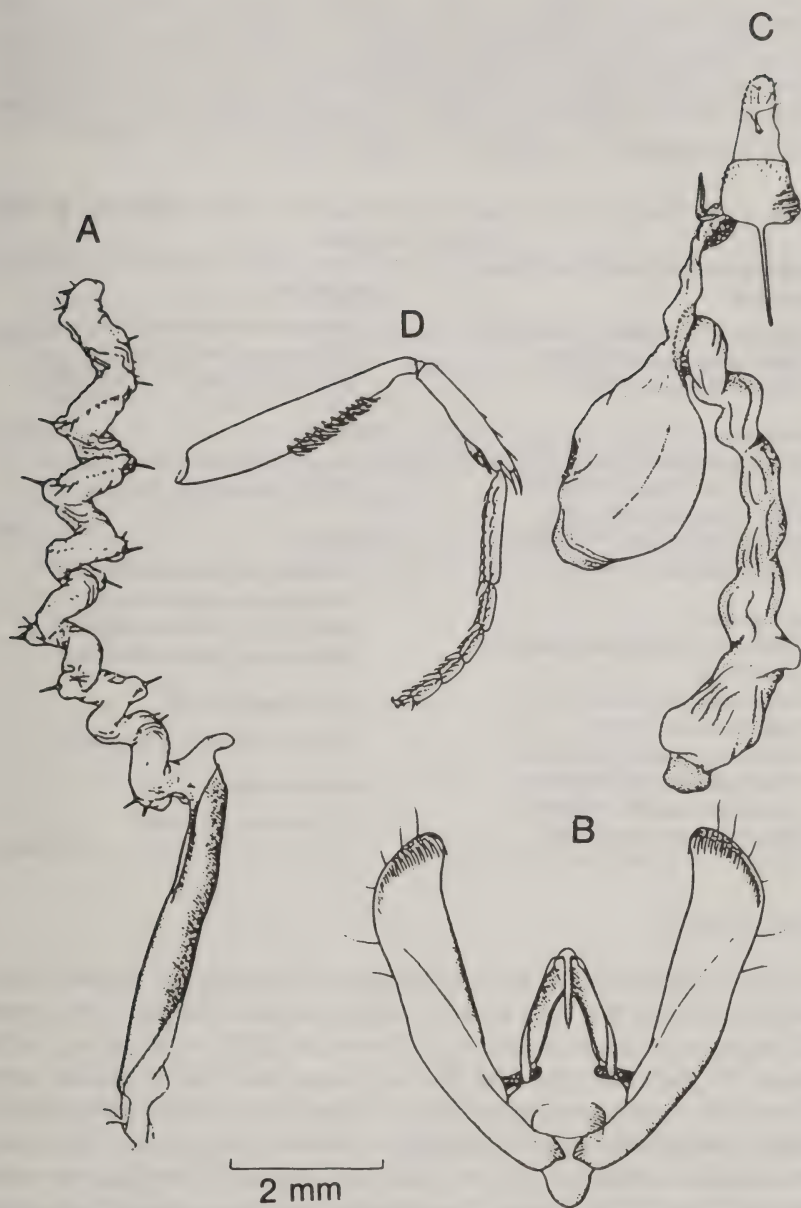
Figure 4. *Helicoverpa armigera* (Hübner): A, B—male genitalia; C—female genitalia; D—right, foreleg.

H. assulta (Guenée) (most of the Old World except for Europe and the Soviet Union—of economic importance), *H. toddi* Hardwick (southern Africa and Madagascar—no known economic importance), and *H. tibetensis* Hardwick (Tibet—no known economic importance). A geographical breakdown of the species of *Helicoverpa* is given in Table 1.

Table 1. *A listing of the species of the genus Helicoverpa by biogeographical region*

Australian	Palaearctic
Helicoverpa punctigera Wallengren	*Helicoverpa armigera* Hübner
Helicoverpa armigera Hübner	*Helicoverpa assulta* Guenée
Helicoverpa assulta Guenée	*Helicoverpa tibetensis* Hardwick
Neotropics	**Oriental**
Helicoverpa bracteae Hardwick	*Helicoverpa armigera* Hübner
Helicoverpa titicacae Hardwick	*Helicoverpa assulta* Guenée
Helicoverpa gelotopoen Dyar	
Helicoverpa atacamae Hardwick	**African**
Helicoverpa zea Boddie	*Helicoverpa armigera* Hübner
	Helicoverpa assulta Guenée
Pacific Islands	*Helicoverpa toddi* Hardwick
Helicoverpa hawaiiensis Quantance and Brues	*Helicoverpa fletcheri* Hardwick
Helicoverpa pallida Hardwick	**South Atlantic Ocean**
Helicoverpa zea Boddie	*Helicoverpa helenae* Hardwick
Helicoverpa confusa Hardwick	
Helicoverpa minuta Hardwick	**North American**
Helicoverpa pacifica Hardwick	*Helicoverpa zea* Boddie
Helicoverpa assulta Guenée	

HELIOTHIS

The genus *Heliothis* is a rather heterogeneous collection of species in both the Old and New Worlds. I am not entirely convinced that all of the groups of species included in *Heliothis* by Hardwick (1970) really belong in the genus. In particular the Old World groups need to be studied more thoroughly. In any case the group most important in the New World is the tobacco budworm complex, *Heliothis virescens* and its allies. This group contains four described species. A key and figures of these four species is given in Todd (1978). Two or three undescribed species possibly also exist in the neotropical regions of South and Central America. The members of the *virescens* complex are easily recognized by the light green coloration of the forewing and the general weakness of the markings on their forewings. In addition to *Heliothis virescens* and *H. subflexa*, there are 10 other species in North America, and perhaps another 20 to 25 species in other

parts of the world. The male genitalia of *H. virescens* and the type-species of the genus, *H. viriplaca*, are shown in Figure 2 for comparison with the male genitalia of *Helicoverpa*. Although a couple of species in Europe are of minor economic importance, only *Heliothis phloxiphagus* (Grote and Robinson) is of any occasional importance in the USA.

REFERENCES

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Hardwick, D.F. 1970. A generic revision of the North American Heliothidinae (Lepidoptera: Noctuidae). Mem. Entomol. Soc. Canada, 73, 59 pp., 114 figures.

Seymour, P.R. 1972. A revision of the genus *Masalia* (Lepidoptera, Heliothidinae). Bull. British Museum (Natural History), Entomology 27(1), 1–100, 10 plates, 113 text figures.

Todd, E.L. 1978. Maculation characters for separation of the species of *Heliothis virescens* complex. Florida Entomologist 61, 197–199.

Distribution and Economic Importance of *Heliothis* spp., Their Natural Enemies, and Host Plants in Egypt

Amira Abd El-Hamid Ibrahim and *Yahia Hussein Fayad**

ABSTRACT

In April 1979, a project was initiated in cooperation with the Office of International Cooperation and Development, U.S. Department of Agriculture, to assess the natural enemies, distribution, seasonal history, and host range of *Heliothis* and *Spodoptera* spp. in Egypt. *Heliothis* spp. were recorded in Egypt for the first time in 1905, on maize. Prior to 1972, only occasional infestations of *Heliothis* were cited on cotton and some wild plants; their study revealed that the genus *Heliothis* was represented in Egypt by three species: *H. armigera* (Hübner); *H. peltigera* (Denis & Schiff.); and *H. nubigera* (Herr-Schaeff). The main host plants of *Heliothis* spp. in Egypt were alfalfa, clover, tomato, green pepper, maize, *Corchorus* sp., cabbage, sweet potato, artichoke, and cotton.

The predominant parasites emerging from field-collected *Heliothis* spp. were larvae of *Microplitis rufiventris* Kok., *Bracon brevicornis* Wesm., *Chelonus inanitus* (L.), *Zele* sp., and *Cotesia* (= *Apanteles*) spp. The number of parasites emerging was low, with the rate of parasitism attaining a maximum of about 6%.

Apparently, parasites contribute little to the suppression of *Heliothis* populations in Egypt. This situation may be attributed to several factors, an important one being the widespread application of insecticides, particularly during the cotton-growing season.

INTRODUCTION

In April 1979, a project, entitled "Biotic Factors Affecting Different Species of the Genera *Heliothis* and *Spodoptera* in Egypt" was initiated between the U.S. Department of Agriculture (USDA) and the Egyptian Ministry of Agriculture to assess the natural enemies, distribution, seasonal history, and host range of *Heliothis* and *Spodoptera* spp. in Egypt. The project was terminated in September 1985.

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In Egypt, cotton is grown on about 1.8–2 million feddan (0.76–0.84 million ha). This crop is attacked by several pests, among them, the cotton leafworm, *Spodoptera littoralis* (Boisd.), and in recent years, *Heliothis* spp. (Noctuidae, Lepidoptera).

Before the introduction of the chlorinated hydrocarbons and the organophosphorus compounds into Egypt, *S. littoralis* was generally controlled by cultural and mechanical measures. Under these conditions, natural enemies contributed to suppression of this pest. Unfortunately, the widespread application of pesticides during the 1950s and 1960s reduced natural enemy numbers. So in 1961, *S. littoralis* caused serious damage to cotton in Egypt.

Heliothis spp. were recorded in Egypt for the first time in 1905, on maize (Willcocks and Bahgat 1937). Until 1972, only occasional infestations occurred on cotton and some other wild plants. These infestations did not cause serious damage, and *Heliothis* never attained pest status. In 1972, a cotton field, consisting of 30 feddan (12.6 ha), 100 km southwest of Cairo, was damaged by a severe infestation of *H. armigera* Hübner. By 1973, infestations were commonly recorded in cotton fields, and severe infestation occurred in Fayoum and Beni-Suef governorates (Upper Egypt) and Demiat and Dakahlia governorates (Lower Egypt). This led to the application of insecticides over about 283,000 feddan (118,860 ha) of cotton during 1974.

In 1976, Ezzat et al. (1976) stated that the name American bollworm had been misapplied to several *Heliothis* spp. in Egypt. Subsequently, a general survey revealed that this group was represented in Egypt by three species, belonging to the genus *Heliothis* Ochsenheimer: *H. armigera; H. peltigera* Denis & Schiff.; and *H. nubigera* Herr-Schaeft (Ezzat et al. 1976). *H. armigera* was classified in the genus *Heliothis,* in spite of the fact that Hardwick (1965) assigned this species as a type for the new genus *Helicoverpa.*

H. nubigera was recorded by El-Zoheiry (1950) as a new pest of watermelon in Egypt. Ezzat et al. (1976) mentioned that *H. armigera* is the most abundant species of *Heliothis* in both Upper and Lower Egypt, where its host plants are crops such as safflower, cabbage, cauliflower, geranium, and okra. *H. peltigera* was found in Upper and Lower Egypt on safflower, chrysanthemum, marsh-flea bean, white musland, and clover. *H. nubigera* was confined to a few localities and a few host plants such as mexian tea, safflower, white musland, and okra, especially in Upper Egypt.

SURVEY OF *HELIOTHIS*

Two main procedures were used to survey *Heliothis* spp. and determine their distribution, host range, and parasites in Egypt. Four governorates—

Kalubia and Dakahlia, representing Lower Egypt; Giza, representing middle Egypt; and Minya, representing Upper Egypt—were chosen for operation of four light traps. The traps were operated every night from sunset to sunrise for 1 year. Traps operated in Kalubia and Dakahlia were replaced with two other traps, operated in Nubaria (Alexandria governorate), Mediterranean coast, and Gemmeiza Research Station (Gharbia governorate), Lower Egypt, for another 2 years.

Mercury vapor bulbs were used in these traps as a light source. Collected insects were checked daily and the *Heliothis* specimens were identified to species.

Larvae of different *Heliothis* spp. were collected from almost all of the governorates of Egypt on different host plants with a sweep net or by hand-picking. Twenty-five larvae from each sample were held under laboratory conditions in individual glass tubes containing artificial diet. The larvae were held at about 27° C and 60% R.H. Parasites emerging from host larvae were collected, mounted, identified, and labeled.

The survey revealed that the genus *Heliothis* is represented in Egypt by the three different species earlier reported by Ezzat et al. (1976). These species (*H. armigera, H. peltigera,* and *H. nubigera*) occur in almost all regions of Egypt. The most prevalent species was *H. armigera,* followed by *H. peltigera* and then *H. nubigera. H. armigera* populations peaked during August and September. However, the maximum number of *H. peltigera* were recorded during April and September, and *H. nubigera* populations peaked during April. *H. armigera* occurred in the light trap catches throughout the year, but few individuals were collected during November, December, and January. During the period of this study, *Heliothis* spp. were not abundant in Egypt, and consequently, they may be viewed as a sporadic pest. The maximum number of *H. armigera* collected was 45, in Giza governorate, in August 1981; of *H. peltigera,* 17, in the Kalubia-Gharbia governorates in September 1981; of *H. nubigera,* 17, in Dakahlia-Alexandria governorates, in February 1982.

PARASITES OF *HELIOTHIS* SPP.

To survey the main parasites of *Heliothis* species, larvae were collected on different host plants and held for parasite emergence. The main host plants of *Heliothis* spp. in Egypt were alfalfa, clover, tomato, green pepper, maize, *Corchorus* sp., cabbage, sweet potato, artichoke, and cotton. The main parasites emerging from the collected larvae were the braconids, *Microplitis rufiventris* Kok., *Bracon brevicornis* Wesm., *Chelonus inanitus* (L.), *Zele* spp., and *Cotesia* (= *Apanteles*) spp.

Of these parasites, *M. rufiventris* appeared to be the most frequent, with the maximum number emerging in May 1980.

Generally, the number of parasites emerging from different species of *Heliothis* were low in proportion to the number of host larvae collected. The rate of parasitism attained a maximum of only 5.8% during the present study, indicating that the parasite complex plays a limited role in controlling *Heliothis* spp. in Egypt. This result may be attributed to several factors, of which a major one is the widespread application of insecticides, particularly during the cotton-growing season (March–October), and the low population of *Heliothis* spp.

Acknowledgment

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Distribution and Economic Importance of *Heliothis* (Lep.: Noctuidae) and of Their Natural Enemies and Host Plants in Australia

P.H. Twine*

ABSTRACT

The pest status and economic importance of the five species of *Heliothis* in Australia are discussed. Two of these species (*H. armigera* and *H. punctigera*) together represent the most serious insect pest of agricultural and horticultural production in Australia. Economic control of these species is achieved solely through insecticide application; however, the recent development of pyrethroid resistance in *H. armigera* has led to the implementation of an insecticide resistance management strategy in eastern Australia to limit any indiscriminate use of these insecticides. The host range of each of the species is discussed. In general both *H. armigera* and *H. punctigera* feed on a wide variety of host plants although there is some preference obvious to particular host groups. The parasite and predator species for *Heliothis* are discussed, particularly in terms of the diversity of niches occupied by each agent and of the notable omissions across host crops and geographical locations. There has been no specific use made of biocontrol agents for commercial *Heliothis* control in Australia, although there are instances where knowledge of their activity is used in pest management systems.

Of the five species of *Heliothis* in Australia, two (*H. armigera* and *H. punctigera*) represent the most serious of all insect pests of field crops throughout Australia. Like many of the *Heliothis* group, these two species are reasonably similar, yet they have distinct characteristics in terms of their phenology and host range. The other three species occur in various areas but have not been recorded as pests to any significant level.

Activity of the two major species is generally restricted to the spring through autumn period in the southern half of the continent, whereas in the more northern (tropical) areas, both species are usually active for most of the year.

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DISTRIBUTION

Very little information on the distribution of *Heliothis* spp. in Australia has been published to-date, but from the available data it would appear that *H. armigera* is somewhat restricted in its distribution. It was originally considered that the species was limited in its activity to the coastal areas (up to 200 km inland) of eastern Australia and the Northern Territory (Common 1953). However, the absence of records of this species from the more inland and western areas was suggested as being associated with limited sampling in these areas. More recently, Zalucki et al. (1985) have proposed that *H. armigera* could be normally present (but rare) in these inland areas and that, with the development of large areas of *Heliothis*-susceptible cropping in these noncoastal areas, there has been an increase in the recording of this species. In more recent times, *H. armigera* has also been recorded in some of the southern states, although, apart from the occasional outbreak in maize, it has rarely developed into a significant problem.

By contrast, *H. punctigera* is endemic to Australia. Common (1953) originally regarded this species as occurring throughout Australia, with the exception of the coastal areas north from Brisbane. Subsequent collections reported by Kirkpatrick (1961), however, have established the distribution of *H. punctigera* throughout the whole of northeastern Australia.

H. assulta has been recorded only from the northern coastal areas of Australia, whereas *H. rubrescens* has been recorded from throughout the continent. *H. prepodes,* the fifth species of *Heliothis* recently described in Australia, has been identified from light trap records only.

Common (1985) described this species from specimens collected in the southern half of the continent only and it has been suggested that the species is endemic to the whole continent.

ECONOMIC IMPORTANCE

Both of the major species of *Heliothis* attack a wide range of economically important plants and the use of insecticides still remains the major method for control of infestations in crops such as cotton, tobacco, tomatoes, sorghum, field peas, sunflowers, navy beans, and soybeans. An estimate of economic loss associated with *Heliothis* activity in Queensland alone during 1979 estimated total losses at A\$16 million annually (Alcock and Twine 1981). This cost was estimated to be split equally between the cost of spraying (both insecticide and application costs) and the value of the residual damage (defined as the loss incurred in spite of a spray application, together with the losses associated with sub-threshold damage). Wilson (1982) subsequently expanded this survey to an Australia-wide base, estimating total Australian loss at A\$23.5 million.

Since the Queensland survey was undertaken, the price of the commonly used insecticides has increased considerably and the acreage of many of the major crops has also increased. Superimposed on these increases has been the implementation of the pyrethroid strategy for control of *H. armigera*. This strategy imposes a voluntary restriction on the use of the less expensive insecticides such as the pyrethroids and endosulfan, and replaces these with the (generally) more expensive organophosphate and carbamate insecticides. Such changes in the economic situation locally would indicate a reassessment of the cost associated with the activity of *Heliothis* in Queensland alone at some A$25 million annually.

This recent example of the cost of the implementation of an insecticide resistance management strategy highlights the economic significance of the development of even low levels of resistance in the *Heliothis* group. With higher levels of resistance developing, the impact of a complete loss of an industry and its associated infrastructure would defy estimation.

HOST PLANTS

The activities of the species in Australia are in keeping with the highly polyphagous nature of the *Heliothis* genus throughout the world. Unfortunately, as with most host lists, the records generally result from the collection of eggs and/or larvae from the plants (usually cultivated crops) concerned. They usually ignore the suitability of the host plant to support complete larval growth and subsequent normal development.

Zalucki et al. (1985) in a recent review of the host plants of *Heliothis* in Australia listed some 161 plant species from 49 plant families as "hosts" for both of the two major pest species. Of these, 33 hosts were recorded as being attacked exclusively by *H. armigera,* 85 by *H. punctigera,* and 43 were attacked by both species. Although these data are recognized as being far from complete, there is the suggestion that *H. punctigera* exploited a wider variety of hosts (39 families), than *H. armigera* (29 families). Although both species have been recorded from many of the crop hosts, *H. armigera* has a tendency to prefer the cereal crops, and *H. punctigera* is restricted to the dicotyledon group of hosts.

For *H. assulta,* the cape gooseberry (*Physalis peruviana*), represents the most significant host. It has also been recorded on tobacco in North Queensland; however, it is not recognized as a serious pest there. Other records indicate that garden pea, maize, and strawberries are occasional hosts to this species.

The host range for *H. rubrescens* is not well defined. However, the species is not recognized as a significant pest of agricultural, horticultural, or floricultural crops.

Common (1985) indicated that no host records were available for *H. prepodes*. He suggested, however, that in view of the evident relationship between the species and the *assulta–zea* species complex, *H. prepodes* might also be assumed to be polyphagous.

PARASITES

The parasites of *Heliothis,* as recorded by several workers, have been reviewed by Zalucki et al. (1985). In summary, the levels of parasitism recorded by the various authors vary considerably between areas, seasons and between host plants. In total these parasites of *Heliothis* included some 14 species of Tachinidae, 7 Braconidae, 1 Chalcidae, 9 Ichneumonidae, 1 Pteromalidae, 1 Scelionidae, and 6 Trichogrammatidae. Of these parasites, each major family group is recorded from at least four of the crop species studied. There has been no record to date of host-plant specificity relationships with parasite species. There are reports, however, of an obvious lower parasitism level from collections of *Heliothis* from maize (Twine, 1975). Differences between parasite listings for each crop probably reflects more the specific geographical location being sampled or the intensity of sampling.

The seasonal distribution of the parasitic species is also variable. Forrester (1981) noted *Heteropelma scaposum* as being of late-season importance, whereas Broadley (1984) did not notice any distinct seasonal pattern of activity for this species. Similarly, the late-season upsurge of *Microplitis* recorded one year by Broadley (1984) was not found to be the case by Forrester (1981).

Eggs

Two general groups of egg parasites are active in Australia.

1. Of the Scelionid group, *Telenomus* sp. is primarily active in the south and central areas of Queensland, although its distribution is probably far more extensive than this.

2. *Trichogramma* spp. are active in the northern areas of the continent, the incidence decreasing within Queensland from north to south. By contrast, the activity of *Trichogrammatoidea* spp. in that state increases towards the southern areas. One notable exception to this generalized distribution north to south across the continent is the reported effectiveness of *Trichogramma ivelae* on *Heliothis* in tomatoes in Victoria (McLaren and Rye 1981). However, the few studies made of egg parasitism levels are insufficient to highlight any trends in the geographical distribution of these species. Titmarsh (1981) found egg parasitism to be unimportant in tobacco areas of North Queensland, although Sloan (1945), Twine

(1973) and Waite (1981) all reported significant egg parasitism rates (up to 65%) in collections from various areas of central and southern Queensland. In the Ord river area of Western Australia, Michael (1973) recorded levels as high as 50%.

Larvae

Microplitis sp. is generally regarded as the predominant parasite of the larval stage in many areas of Australia, with very high levels of parasitism being recorded in crops such as sunflower and tobacco. Broadley (1981) reported this species as contributing most (2–20%) to the total parasitism recorded (21–36%) over a 3-year study in sunflowers. Similarly, Titmarsh (1981) recognized the species as one of the major mortality factors for *Heliothis* larvae in tobacco. Forrester (1981) reported parasitism levels by *Microplitis* sp. as varying from 3–10% throughout the summer-autumn period over four seasons (1976–79).

Pupae

Several studies have indicated that parasites emerging from the pupal stage constitute a significant proportion of the total parasite complex. Of these, *H. scaposum* and *Carcelia noctuae* are the two most commonly recorded parasites. Forrester (1981) attributed an average of 23% parasitism (based on a 4-year period) to *H. scaposum* late in the season (May). He further reported that the Tachinidae group contributed an average (for the same 4-year period) of 28% parasitism during January. Kay (1982) also reported 12–16% parasitism by *H. scaposum* from *Heliothis* collected on sunflower in southeast Queensland. Finally, Broadley (1984) recorded *H. scaposum* parasitism levels ranging from 7–11% over a 3-year study on sunflower.

Both major species groups of parasites have also been collected from most of the major crop hosts.

PREDATORS

Numerous lists of predatory species have been reported for the crops capable of supporting high *Heliothis* populations. Zalucki et al. (1985) have listed some 29 species as being reported by at least one author as suspected predators. Room (1979) actually noted some 500 species of arthropods in cotton in New South Wales, although he lists 41 predaceous insect and spider species. Of these, evidence of predation was reported for 19 only. By contrast, Evenson and Basinski (1973) listed very few beneficial species in the Ord River area of western Australia, but, Wilson et al. (1972) and Michael (1973) listed more. Amongst the Insecta group of predators, most species have been collected from a majority of the host crops, supporting the theory of the generalized feeding habits of these species.

Nabis capsiformis is the most frequent of the predatory species recorded, with general predator activity being reported greatest in areas where insecticide usage is low and where there is an abundant supply of unsprayed crops supporting alternative prey. *Geocoris lubra* and *Deracocoris signatus* are also abundant predators, particularly in cotton, sorghum, sunflower, and soybean crops.

Among the published lists of predatory species is a notable absence of records for *Orius* spp. in cotton crops (Room 1979). This contrasts with the records of very high numbers of the species collected from adjacent sunflower crops (Broadley 1981; Forrester 1981) in many of the mixed cropping areas of eastern Australia.

Perhaps the most underestimated group of predators recorded in many of the agricultural crops is the spiders. Broadley (1981) and Room (1979) both reported ten species of spiders in sunflower and cotton, respectively. Bishop and Blood (1977) recorded some 23 species in cotton crops in south east Queensland.

The overall significance of these beneficial species to *Heliothis* population dynamics is not understood, a phenomenon perhaps not uncommon throughout the world, but which we are attempting to rectify. Room (1979) has attempted to use radio-tracer techniques to identify predaceous species. However, all other predator studies have relied on the reported feeding habit of each species in assessing its status as a predator. The change in attitude that has developed locally regarding the value of some of the mirid species, originally as predatory and more recently as phytophagous, is an example of the need to proceed with caution in the use of this technique.

Very few attempts have been made to ultimately assess the true value of the biocontrol agents recorded in *Heliothis*-susceptible crops, particularly as they affect the population dynamics of the pest. Room (1979) has made some estimates of the mortalities acting on the various life stages of *Heliothis* in unsprayed cotton. However, Titmarsh (1981) has provided the only detailed life tables for *Heliothis* in Australia. Unfortunately, the economics of tobacco and the present attitudes towards pest control in that industry will ensure that the data from this study have very little promise of ever being used in a commercial sense. With such a heavy reliance on insecticides in this country for the commercial control of *Heliothis,* the urgent need for an assessment of the natural mortality factors, and particularly the biotic factors, cannot be overemphasized.

Reasonably sound approaches to pest management have already been developed in some cropping systems (sorghum and cotton). Each of these has recognized the role of naturally occurring biocontrol agents to some extent. However, there are many other cropping systems for which such pest management approaches could be developed in which spray decisions

are based not only on economic analyses of the costs involved, but where the importance and role of the biological system are included as well. Optimum use of the cost-free activity of these biocontrol agents can only be made through study of field life tables.

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Distribution and Economic Importance of *Heliothis armigera* and Its Natural Enemies in China

Ma Shijun and *Ding Yanquin**

The cotton bollworm, *Heliothis armigera* Hübner, is distributed throughout the cotton-growing region of China, causing the greatest damage in the Yellow River and Yangtze River basins. The most effective natural enemy is the predator, *Orius similis*. A mathematical model has been developed to estimate the attack efficiency of *O. similis*. Economic injury levels and economic thresholds for bollworm have been worked out, based on field experiments on the compensation ability of cotton, life tables of the pest, phenology of the cotton crop, and control costs. A new economic threshold, higher than previously used ones, was proposed and widely tested. This was found to reduce control costs, increase cotton yield by about 15%, and protect natural enemies of the bollworm through reduced insecticide use.

The cotton bollworm, *Heliothis armigera* Hübner, is distributed through all of the cotton-growing regions of China. It is an important pest in the principal cotton-growing regions (Figure 1). Its main host plants are cotton, corn, wheat, peanut, and tomato. In the Liao River basin and inland basin of northwest China, the bollworm has three generations each year; in the Yellow River basin and in the Yangtze River basin, four to five generations are completed each year. In south China, depending on local climatic conditions, six to eight generations may occur.

The period when the cotton plant is susceptible to damage by the bollworm differs between regions. The population density of bollworm and damage to cotton are highest in the Yellow River basin. There, the second generation of the bollworm causes the greatest damage to cotton squares during late June to mid-July. In the Yangtze River basin, damage is also serious. However, the fourth generation is the most damaging to cotton bolls from late August to mid-September. In south China, damage to cotton by the bollworm is not viewed as serious.

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Figure 1. Distribution of *Heliothis armigera* in the major cotton-producing regions of China: I. Yellow River basin; II. Yantze River basin; III. Liao River basin; IV. Inland cotton region; V. South China cotton region.

NATURAL ENEMIES OF THE BOLLWORM

The most efficacious natural enemy of the bollworm in China is the predator *Orius similis* (Anthocoridae). Other natural enemies are listed in Table 1.

POPULATION DYNAMICS OF THE BOLLWORM AND THE EFFECT OF NATURAL ENEMIES

Yangtze River Cotton-growing Region

The population dynamics of the bollworm are shown in Table 2, based on the life tables of bollworm (second generation) under natural conditions during the second to the fourth generation (1980–84). The survivor rate curves of the population reveal that the mortality was greatest in the early growth stages (including eggs and first- to third-instar larvae). Cumulative mortality was 98%.

Table 1. *Natural enemies of* Heliothis armigera *in China*

Orius similis	(Anthocoridae)
Campoletis chlorideae Uchida	(Ichneumonidae)
Netelia sp.	
Enicospilus sp.	
Meteorus sp.	(Braconidae)
Ophion luteus Linnaeus	(Ichneumonidae)
Microplitis sp.	(Braconidae)
Trichogramma confusum Viggiani	(Trichogrammatidae)
T. dendrolimi Matsumura	(Trichogrammatidae)
Charops bicolor (Szepligeti)	(Ichneumonidae)
Polistes antennais Perez.	(Vespidae)
Meteorus japonicus Ashmead	(Braconidae)
Geocoris tricolor Fabr.	(Lygaeidae)
Adonia variegata (Goeze)	(Coccinellidae)
Coccinella septempunctata Linnaeus	(Coccinellidae)
Propylea japonica (Thunberg)	(Coccinellidae)
Chrysopa sinica Tjeder	(Chrysopidae)
C. septempunctata Wesmael	(Chrysopidae)
C. formosa Brauer	
C. phyllochroma Wesmael	
Nabis sinoferus Hsiao	(Nabidae)
Polistes oflivacens Degeer	(Vespidae)
Calosoma maserae chinense K.	(Carabidae)
Pheropsophus occitalpitalis (Macleag)	(Carabidae)
Euborellia palipes Shiraki	(Psalididae)
Misumenops tricuspidatus (Fabricius)	
Erigonidium graminicola	
Pardosa T-insignita (Bois et Str.)	(Lycosidae)
Theridion octomaculatum	(Theridiidae)
T. angulithora (Bois et Str.)	(Theridiidae)
Chiracanthium pennyi O.P. (Cambride)	(Clubionidae)
Erigonea dengipalis (Wider)	(Erigonidae)
Oedothorax insecticeps Bois.	
Bufo sp.	

The death of eggs and larvae was due to the following conditions: (a) unfavorable weather; (b) predation or parasitism by insects or spiders; and (c) other factors. At the egg stage, weather conditions were important. In the larval stage, mortality was higher in the first to third instars than in later instars. Continuous observation in cotton fields has revealed that predators, particularly *O. similis,* cause the highest larval mortality. About 13% mortality was attributed to predators. Parasitism was a secondary mortality factor. Pupal death was mainly due to moisture in the soil. The highest growth rate of population was about 1.9-fold in the third generation. However, it was only 0.39-fold in the second generation and 0.5-fold in the fourth generation. The fourth generation of the cotton bollworm population is the most damaging generation in this cotton area.

Table 2. Natural life table of second generation cotton bollworm in Nantong (1979–1982) (Plant Protection Station of Nantong, China)

Cause of death (dxp)	Developmental stage and death rate								
	Egg mortality	Larval mortality						Pupal mortality	Total
		1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar		
No. at start of stage lx	1000	357.60	67.3628	37.3684	22.390	5.9484	2.758		
Disappearing	0.0919	0.2213	0.1014	0.1091	0.1006	0.1483	0.1442	0.639	185.5143
Wind and rain	0.3799	0.037	0.0262	0.0256	0.0225	0.0283			396.5060
Preyed on by									
Orius similis	0.062	0.1734	0.0164	0.0030					125.4065
Misumenops tricuspidatus	0.003	0.1213	0.1535	0.1128	0.1158	0.0495	0.0038		64.2085
Erigonidium graminicola	0.008	0.0721	0.0537	0.0374	0.0284	0.0010			39.4108
Other predators	0.0009	0.0265	0.0215	0.0171	0.0995	0.2369	0.5941	0.0715	17.1013
Total	0.0745	0.3887	0.2451	0.1703	0.2437	0.2880	0.598	0.0715	246.1277
Parasitized by									
Trichogramma sp.	0.0551								55.1342
Campoletis chlorideae			0.0178	0.0559	0.3268	0.0487			10.9064
Other parasitoids					0.0007				0.0146
Total	0.055		0.0178	0.0559	0.3275	0.0487			66.0552
Other causes									
Diseases		0.1601	0.0497		0.0227	0.0155	0.0184	0.0124	62.1559
Nonfertilization	0.041	0.0019							40.9752
Loss with shedding of fruits			0.0052	0.0162	0.0167	0.0075	0.0152		2.0802
Soil water content								0.1444	0.0923
Total	0.642	0.8116	0.5937	0.401	0.7434	0.5363	0.7683	0.2283	999.563

A mathematical model of the attack efficiency of *O. similis* on cotton bollworm eggs under different temperatures shows that the response curve of attack efficiency with temperatures is s-shaped in the intermediate range, but declines rapidly near the extremes (minimum and maximum threshold temperatures). Based on this trend, some hypotheses were formulated and a mathematical model of attack efficiency in the whole range between the two threshold temperatures is given as

$$E = \frac{K}{1 + \exp\left[-r(T - T_f)\right]} \left[1 - e^{-\left(\frac{T - T_L}{\delta_1}\right)^2}\right] \left[1 - e^{-\left(\frac{T_H - T}{\delta_2}\right)^2}\right],$$

where E denotes the attack efficiency (attack rate); T = temperature; r, k, T_f, T_L, δ_1 and δ_2 are parameters; r = the intrinsic attack rate; k = the potential saturation of attack rate; T_f = the optimal temperature at which the rate of change of the attack efficiency with respect to temperature is maximum; T_L = the lowest threshold temperature, T_H = the highest threshold temperature; and δ_1 and δ_2 the extent about the two threshold temperatures where attack efficiency declines.

With the data on *O. similis,* these parameters in the equation are estimated by Marquardt's method of damped least squares (RMS error = 0.003).

From simulation results we obtained k = 0.4818, r = 0.2020, T_f = 24.5755, T_L = 11.9633, T_H = 38.0531, and δ = 1.9793; thus

$$E = \frac{0.4818}{1 + \exp\left[-0.2020(T - 24.5755)\right]} \left[1 - e^{-\left(\frac{T - 11.9633}{1.9793}\right)^2}\right] \times$$

$$\left[1 - e^{-\left(\frac{38.0531 - T}{1.9793}\right)^2}\right].$$

This mathematical model not only describes the regularity of attack behavior of *O. similis* under different temperature conditions, but also enables us to estimate some parameters which could not be estimated in the laboratory, such as T_f, T_L, T_H and δ.

Yellow River Cotton Region

According to the life tables of bollworm populations under natural conditions from the second to third generations (1978–81), major mortality occurs between the egg stage and the third-instar larval stage. Cumulative mortality during this period is nearly 90%. This illustrates that the survivor rate for the bollworm population of the second generation in this cotton

area is higher than in the Yangtze River area; thus the second generation of cotton bollworm is the one that causes the most damage in the Yellow River area (Table 3).

Table 3. Natural life table of second generation cotton bollworm in Hobei, China (1978–1981) (Mengwen 1981)

Developmental stage	No. of individuals at start stage (lx)	Cause of death (dxp)	No. dying during the stage (dx)	Mortality of the stage (qx)	Survivor rate of the stage	Cumulative mortality
	903	Disappearing	357	0.3953		
		Desiccating	103	0.1141		
Egg stage		Parasitized	1	0.0011		
		Preyed on	8	0.0089		
Egg stage total			469	0.5194	0.4806	0.5194
Larval stage						
1st instar	434	Unknown	180	0.4147		
		Preyed on	1	0.0023		
		Total	181	0.4170	0.5830	0.7198
2nd instar	253	Unknown	91	0.3597	0.6403	0.8206
3rd instar	162	Unknown	78	0.4815		
		Parasitized	1	0.0062		
		Total	79	0.4877	0.5123	0.9081
1–3 instar total			351	0.8088	0.1912	
4th instar	823	Unknown	29	0.3494		
		Parasitized	5	0.0602		
		Total	34	0.4096	0.5904	0.9457
5th instar	49	Preyed on	8	0.1632		
		Parasitized	1	0.0204		
		Total	9	0.1836	0.8164	0.9557
6th instar	40	Preyed on	23	0.5750	0.4250	0.9812
4–6 instar total			66	0.7951	0.2049	
Larval stage total			417	0.9608	0.0392	
Pre-pupal stage	17	Parasitized	2	0.1176	0.8824	
Pupal stage	15	Parasitized	1	0.0667	0.9333	0.9845
Adult stage	14					

The chief natural enemies of the cotton bollworm in this region are: *Erigonidium graminicola*, *Chrysopa sinica*, and *Nabis sinoferus*. Predation of the bollworm along with another predator, the dwarf spider, was studied in a simulation model (Li et al. 1983). A simulation model of the interaction of the dwarf spider and the bollworm was proposed:

$$\begin{cases} N_{t+1} = N_t \left[1 + r(1 - N_t/K)\right] \exp\left[-adP_t^{t-m}/1 + aT_hN_t\right] \\ P_{t+1} = adBN_tP_t^{1-m}/(1 + aT_hN_t) + xP_t \end{cases}$$

Model A

$$N_{1,t+1} = N_{1,t} \left[1 + r_1 \left(1 - \frac{N_{1,t}}{K_1} \right) \right] \exp \left(- \frac{EQ_1}{N_{1,t}} \right)$$

$$N_{2,t+1} = N_{2,t} \left[1 + r_2 \left(1 - \frac{N_{2,t}}{K_2} \right) \right] \exp \left[- \frac{E(1-Q_1)}{N_{2,t}} \right]$$

$$P_{t+1} = EBQ_1 + x \ P_t$$

where $E = \dfrac{dP_t^{1-m} \sum F_i a_i \sum N_{i,t}}{1 + \sum F_i a_i \sum F_i T_{hi} \sum N_{1,t}}$, $Q = \dfrac{C_1 F_1}{C_1 F_1 + 1 - F_1}$.

Model B

$$N_{1,t+1} = N_{1,t} \left[1 + r_1 \left(1 - \frac{N_{1,t}}{K_1} \right) \right] \exp \left(- \frac{EQ_1}{N_{1,t}} \right)$$

$$N_{2,t+1} = N_{2,t} \left[1 + r_2 \left(1 - \frac{N_{2,t}}{K_2} \right) \right] \exp \left[- \frac{E(1-Q_1)}{N_{2,t}} \right]$$

$$P_{t+1} = BN_{1,t} \left[1 - \exp \left(1 - \frac{EQ_1}{N_{1,t}} \right) \right] + x \ P_t$$

Model C

$$N_{1,t+1} = N_{1,t} \ \exp \left[r_1 \left(1 - \frac{N_{1,t}}{K_1} \right) \right] \exp \left(- \frac{EQ_1}{N_{1,t}} \right)$$

$$N_{2,t+1} = N_{2,t} \ \exp \left[r_2 \left(1 - \frac{N_{2,t}}{K_2} \right) \right] \exp \left[- \frac{E(1-Q_1)}{N_{2,t}} \right]$$

$$P_{t+1} = EBQ_1 + x \ P_t$$

Model D

$$N_{1,t+1} = N_{1,t} \ \exp \left[r_1 \left(1 - \frac{N_{1,t}}{K_1} \right) \right] \exp \left(- \frac{EQ_1}{N_{1,t}} \right)$$

$$N_{2,t+1} = N_{2,t} \ \exp \left[r_2 \left(1 - \frac{N_{2,t}}{K_2} \right) \right] \exp \left[- \frac{E(1-Q_1)}{N_{2,t}} \right]$$

$$P_{t+1} = BN_{1,t} \left[1 - \exp \left(1 - \frac{EQ_1}{N_{1,t}} \right) \right] + x \ P_t$$

The research results reveal that: (1) with the increase of the interference between predator individuals, the equilibrium population densities of the prey will go up, and of the predator will decline; (2) describing the population logistic growth form with the differential equation $N_{t+1} = N_t [1 + r (1 - N_t/K)]$ will make the model more stable than with the equation

$N_{t+1} = N_t \exp [r(1-N_t/K)]$; (3) calculating the amount of prey captured, using the equation $N_{a1} = N_t [1-\exp(-EQ_t/N_t)]$ increases the stability of the model more than using the equation $N_{a1}-EQ_1$.

ECONOMIC INJURY LEVELS AND ECONOMIC THRESHOLDS OF BOLLWORMS ON COTTON

As Table 4 shows, less than half the squares produced by the cotton plant mature into bolls. In the Yellow River area, the bollworm is the main pest on cotton, and it is the chief cause of shedding of squares; consequently, this is also the stage requiring insecticidal control measures.

In order to understand the ability of cotton to compensate for early shedding and the economic injury level of bollworm, two kinds of experiments were conducted in cotton fields from 1980–85: (1) artificial removal of fruits from cotton plants by hand, i.e., a form of simulated injury; (2) natural damage caused by bollworm which had to be augmented by artificially infesting the plants with varying densities of eggs and larvae. So, varying levels of fruit loss and damage were caused. Yields were measured after a specific length of time.

Table 4. Phenological table of the cotton crop in North China

Year	Developmental stage of plant	No. squaring	No. squares shed	Cause of shedding	% shedding
1980	Square stage (mid-June to mid-July)	232			
			40	Physiological shedding	0.172
			44	Bollworm injury	0.192
			4	Other pest injury	0.017
		232	88		0.379
	Boll stage (late July to late August)		207	Physiological shedding	0.418
			17	Bollworm injury	0.034
			7	Other pest injury	0.014
		495	231		0.467
1981	Square stage (mid-June to mid-July)	248			
			28	Physiological shedding	0.113
			41	Bollworm injury	0.165
			2	Other pest injury	0.008
		248	71		0.28
	Boll stage (late July to late August)	487			
			251	Physiological shedding	0.515
			21	Bollworm injury	0.043
			18	Other pest injury	0.037
		487	290		0.595
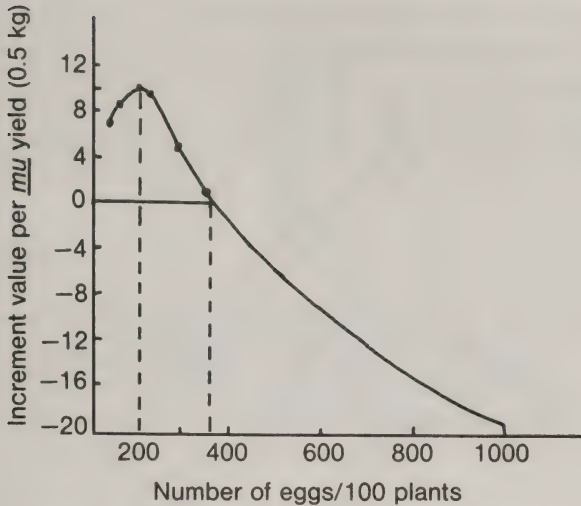
Figure 2. Economic threshold levels for *Heliothis armigera* on cotton in China.

The trials on the artificial removal of fruits at different development stages revealed that the cotton plants have the ability to compensate for an early loss of fruits. The compensation was very high during the first 3 weeks of the square stage, but declined during the boll stage. When two to eight fruits were removed by hand in the first week of July, the yield of cotton always increased with the number of fruits removed in the highly fertilized cotton fields, but compensation was lower in the less fertile fields and at the boll stage.

The relationship between *Heliothis* egg number per 100 plants and yield of cotton per unit area can be expressed as in Figure 2; yield increases as egg densities increase; however, when egg densities were above 350 per 100 plants, yield declined quickly.

The relationship among density of bollworm larvae, the number of fruits damaged, and the survivor percentage, as illustrated in Figure 3, revealed that:

1. The most damaging stage of the bollworm is the second- to third-instar larva, which accounts for 65% of the total number of fruits damaged.

2. Older larvae—fourth- to sixth-instar—are cannibalistic; hence, the survival rate of larger larvae and damage levels decreases as the densities of larvae increase; e.g., when larval density is $4/m^2$, mortality is 50% after 4 days; the number of damaged fruits with this larval density is 20% less than with a single larva over a similar area. With a larval density of $12/m^2$, the mortality rises to 90%; at the same time, the degree of damage drops to one-third that caused by a single larva. In short, shedding of several squares caused by the bollworm results in a per unit yield increase without a reduction in the quality of the cotton.
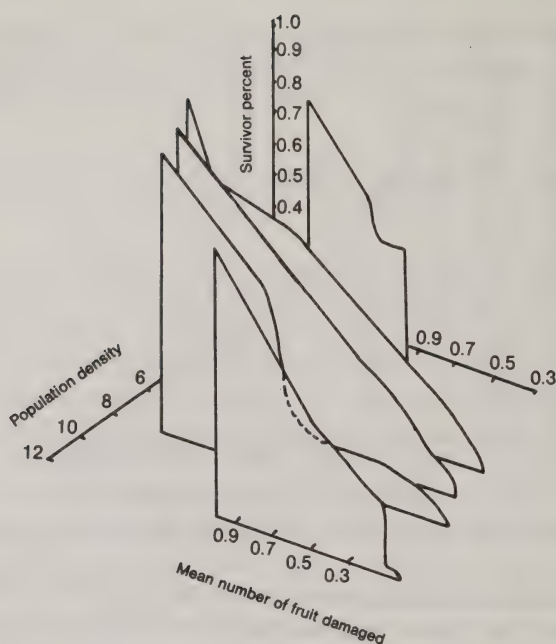
Figure 3. Relationship between the population density of *Heliothis armigera* larvae, number of fruit damaged, and survivor percent.

On the basis of results obtained from field experiments on the compensation ability of cotton, life tables of pest and host plant, economic injury level, and control costs, a new economic threshold was proposed (Table 5); this threshold is much higher than the normal control threshold. The new index was demonstrated and tested widely in 1983–84.

Using this economic threshold, managers not only saved on control

Table 5. Comparison of cotton yields with economic thresholds of 300 and 15 bollworm eggs per plant in China[1]

Year	Cotton variety	Mean no. of large bolls/plant		Mean no. of unopen bolls/plant		Yield increase (%)	
		I	CK	I	CK	I	CK
1983							
	Lu 1	23.32	20.47	1.05	2.32	18.30	0.00
	Jie 4	22.64	20.83	1.14	2.17	11.43	0.00
1984							
	Jie 7	17.26	14.88	0.12	0.49	19.11	0.00
	Jie 4	19.92	16.16	0.24	0.58	13.62	0.00

[1] I = Treatment begins when cumulative egg level is 300 eggs/plant.
CK = Treatment begins when cumulative egg level is 15 eggs/plant.

costs but also increased cotton yield by more than 15% over the usual practice. The lower insecticide use also protected natural enemies of the bollworm. These natural enemies were important in controlling the bollworm and other insect pests as well as in improving the ecological environment of cotton fields by reducing the amount of insecticides applied to cotton in China (Sheng 1985).

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Economic Importance of *Heliothis* spp. in India and an Assessment of Their Natural Enemies and Host Plants

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ABSTRACT

Comprehensive lists of host plants, parasitoids, and predators of *Heliothis armigera* (Hübner), *H. assulta* Guenee, and *H. peltigera* Schiffermuller recorded in India are presented and their status reviewed. The hosts of *H. armigera* include 181 cultivated and wild plant species. *H. armigera* is the most abundant species, and is currently of great economic importance on pigeonpea, chickpea, tomato, and cotton; it is expected to become important on sorghum, pearl millet, maize, tobacco, and groundnut in the near future. *H. assulta* and *H. peltigera* are mostly restricted to weeds.

Altogether, 77 parasitoids on *H. armigera*, 13 on *H. assulta*, and 16 on *H. peltigera* have been reported from India. The most important parasitoids of *H. armigera* include the hymenopterans *Trichogramma chilonis* Ishii, *Campoletis chlorideae* Uchida, and *Eriborus* sp.; the dipterans *Carcelia illota* (Curran) *Goniophthalmus halli* Mesnil, and *Palexorista laxa* Curran; and the nematodes *Ovomermis albicans* (Siebold) and *Hexamermis* sp. The total number of predators recorded on *Heliothis* spp. is 33. This paper highlights the importance of crop influences on parasitoid incidence.

INTRODUCTION

The genus *Heliothis* (Lepidoptera: Noctuidae) is widely distributed over the tropics and subtropics. It is represented by several species which are among the most dreaded agricultural pests, for they have defied human efforts to check their spread and consequent economic damage to several

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important crops. The fact that several national and international conferences—including the present one—have been held to discuss this genus reflects its importance. In this paper, the distribution and economic importance of *Heliothis* spp. in India and an assessment of the importance of their natural enemies and host plants are briefly reviewed and discussed.

HELIOTHIS COMPLEX IN INDIA

It is generally believed that three species of *Heliothis* occur in India (Figure 1): *H. armigera* (Hübner), *H. assulta* Guenée, and *H. peltigera* Schiffermuller. However, Bhattacherjee and Gupta (1972) described one more species, *H. rama,* infesting cotton and pigeonpea, and provided a taxonomic key to distinguish between the four species. No subsequent reference to this species is available. Further, Bhattacherjee (1972) recognized three subspecies of *H. armigera,* on the basis of slight differences in the male genitalia: (1) *H. armigera armigera* attacking pulses (pea, chickpea) and tomato; (2) *H. armigera sorghi,* attacking cereals (wheat, sorghum, maize); and (3) *H. armigera hibisci,* attacking malvaceous crops (cotton, okra). He reported these species as possessing 13, 12, and 11 aedeagal cornutal spines, respectively.

But Jadhav et al. (1985) found no such differences in aedeagal cornutal spines among large populations of *Heliothis* collected and reared on sorghum, pigeonpea, and chickpea, and also in those collected from light traps; therefore these authors disagreed with the basis of erecting the above subspecies.

Notwithstanding these studies, puzzling differences do exist in the behavior of *Heliothis* populations infesting various host plants; so much so, that the existence of at least subspecific differences between populations cannot be completely ruled out (Reed and Pawar 1982). It was observed in the laboratory at the Commonwealth Institute of Biological Control (CIBC), Bangalore, that an introduced tachinid, *Eucelatoria bryani* Sabrosky (earlier misidentified as *E. armigera* Coq.), readily parasitized *Heliothis* larvae collected from tomato fields, but rejected those from maize fields (Manjunath 1968, unpubl.). Whether this behavior of the parasite was influenced by host plant or indicated the existence of possible subspecies was not clear. Probing studies are still warranted to solve the "*Heliothis* puzzle." Until such time, we will treat *H. armigera, H. assulta,* and *H. peltigera* as the species present in India.

DISTRIBUTION OF *HELIOTHIS* SPP.

All three species of *Heliothis* have been reported from most of the states
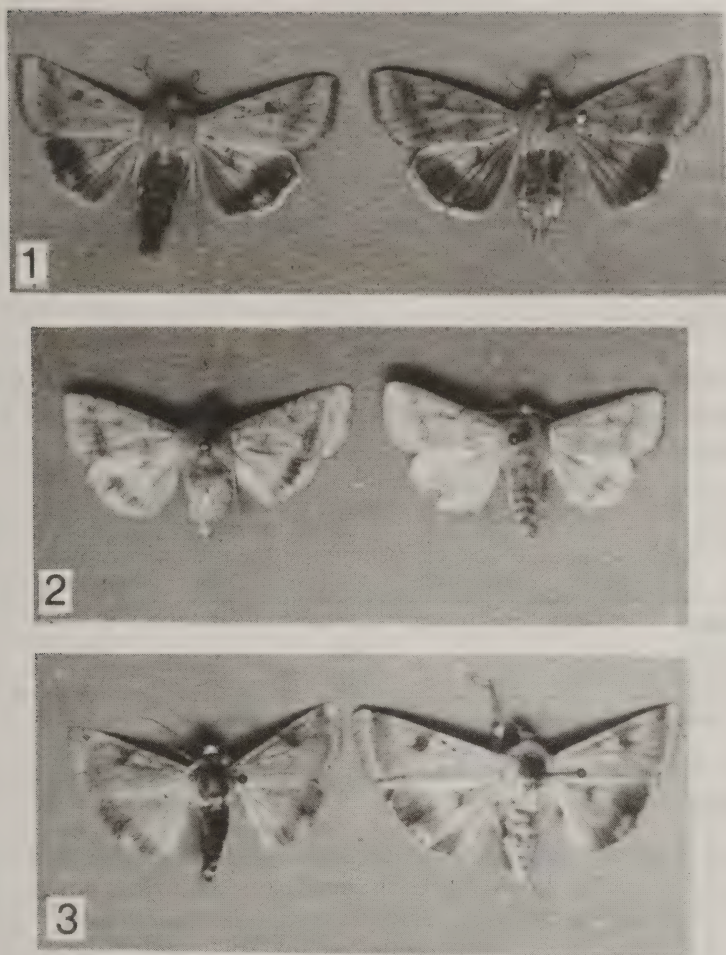
Figure 1. *Heliothis* species recorded in India.
Left: male. Right: female.
1—*H. armigera* (Hübner)
2—*H. assulta* Guenée
3—*H. peltigera* Schiffermuller

and Union Territories of India, ranging from the tropical Andaman and Nicobar Islands to temperate Jammu and Kashmir; *H. armigera* is by far the most common species.

Light-trap studies conducted during 1977–84 in northern India at Hissar, Haryana (29° N), and southern India at Patancheru, Andhra Pradesh (18° N), revealed that over 90% of the total catch was comprised of *H. armigera* (Table 1). This probably reflects the relative populations of the three species in other parts of India also.

Table 1. Percent average annual catch of Heliothis *spp. in light traps at two locations in India, ICRISAT, 1977–84*

Trap location	H. armigera	H. assulta	H. peltigera
Hissar (29° N) (Haryana)	92.4 ± 2.51	6.1 ± 2.17	1.5 ± 0.67
Patancheru (18° N) (Andhra Pradesh)	99.2 ± 0.10	0.6 ± 0.06	0.2 ± 0.06

HOST PLANTS AND CROP DAMAGE

A consolidated list of host plants of *H. armigera, H. assulta,* and *H. peltigera,* indicating the status of each host, is presented in Table 2, and summarized below:

Heliothis species	Plant families		Total	No. of plant species as important hosts		Total
	Dicot	Monocot		Dicot	Monocot	
H. armigera	40 (169)[a]	5 (12)	45 (181)	18	3	21
H. assulta	3 (7)	—	3 (7)	3	—	3
H. peltigera	5 (7)	—	5 (7)	4	—	4

[a]Figures in parentheses show total number of plant species.

Plants fed upon by *H. assulta* and *H. peltigera* are also fed upon by *H. armigera.*

Table 2. Recorded host plants of Heliothis *spp. in India. The families are arranged according to phylogeny in accordance with Hutchinson (1973).* HA *=* H. armigera (*Hübner*), HP *=* H. peltigera *Schiffermuller,* HAS *=* H. assulta *Guenée.*
+ *= of doubtful or no importance, 1 = of minor importance, 2 = important host, 3 = very important host.*

Order, family, genus, and species of host plant	Species recorded			Reference*
	HA	HP	HAS	
DICOTYLEDONS				
1 ROSALES				
1.1 ROSACEAE				
Amygdalus communis L.	+			10
Fragaria vesca L.	+			24
Rosa banksiana R.Br.	+			7
Rosa sinensis Jacq.	1			5
2 LEGUMINALES				
2.2 CAESALPINIACEAE				
Cassia tora L.	+			5

Order, family, genus, and species of host plant	Species recorded			Reference*
	HA	HP	HAS	
2.3 MIMOSACEAE				
Acacia catechu Willd.	+			14
Albizia procera (Willd.) Benth.	+			14
2.4 FABACEAE (LEGUMINOSAE)				
Aeschynomene indica (L.)	+			16
Alysicarpus rugosus (Willd.)	+			10
Arachis hypogaea L. (Groundnut)	3	+		7, 13
Atylosia albicans W. & A.	+			10
Atylosia cajanifolia Haines	+			10
Atylosia lineata W. & A.	+			10
Atylosia platycarpa Benth.	+			10
Atylosia scarabaeoides (L.) Benth.	+			10
Atylosia sericea Benth. ex. Bak.	+			10
Cajanus cajan L. (Pigeonpea)	3			7
Cicer arietinum L. (Chickpea)	3			7
Clitoria ternatea L.	+			10
Crotalaria alba L.	+			10
Crotalaria juncea L. (Sunnhemp)	+			7
Crotalaria retusa L.	+			5
Dalbergia sissoo Roxb.	+			14
Desmodium tortuosum (SW) Dc.	+			21
Glycine max (L.) Merrill (Soybean)	2			7
Indigofera tinctoria L.	+			7
Lablab purpureus L. (Hyacinth bean)	+			7
Lathyrus odoratus L.	1			2
Lathyrus sativus L. (Chickling vetch)	+			7
Lens culinaris Medik. (Lentil)	+			2
Macrotyloma uniflorum (Lam.) Verdc. (Horsegram)	1			7
Medicago sativa (L.) (Alfalfa)	1			7
Melilotus indica L.	+			21
Phaseolus aconitifolius Jacq.	1			21
Phaseolus lunatus L. (Lima bean)	+			24
Psophocarpus tetragonolobus (L.) Dc.	1			19
Phaseolus vulgaris L. (Haricot bean)	1			21
Pisum sativum L. (Pea)	2			7
Rhynchosia minima (L.) Dc.	+			5
Sesbania bispinosa (Jacq.) W.F. Wight	+			10
Tephrosia purpurea Pers.	+			2
Trifolium alexandrinum L. (Berseem)	1			21
Vicia sativa L. (Common vetch)	+			21
Vigna mungo (L.) Hepper. (Black gram)	1			10
Vigna radiata (L.) Wilczek (Green gram)	2			5
Vigna unguiculata (L.) Walp. (Cowpea)	2			21
3 URTICALES				
3.1 CANNABACEAE (CANNABINACEAE)				
Cannabis sativa L. (Hemp)	+			7

Order, family, genus, and species of host plant	Species recorded			Reference*
	HA	HP	HAS	
3.2 URTICACEAE				
Ficus carica L.	+			20
4 CAPPARALES				
4.5 CAPPARIDACEAE				
Cleome (= *Gynandropsis*) *gynandra* Briq.	2			5
4.6 MORINGACEAE				
Moringa oleifera Lam.	1			31
5.7 VIOLACEAE				
Viola tricolor L.	1			14
6 CUCURBITALES				
6.8 CUCURBITACEAE				
Cucurbita maxima Duch. Ex. Lam. (Pumpkin)	+			24
Cucurbita pepo L. (Summer Squash)	1			8
Cucumis sativus L. (Cucumber)	1			26
Lagenaria vulgaris Ser. (Bottle gourd)	1			10
Momordica charantia L. (Bitter gourd)	1			33
Trichosanthes cucumerina L. (Snake gourd)	+			1
7 TILIALES				
7.9 TILIACEAE				
Corchorus aestuans L.	+			10
Corchorus olitorius L. (Jute)	+			3
Corchorus trilocularis L.	+			10
Triumfetta pilosa Roth.	+	2		17
7.10 BOMBACACEAE				
Fremontia mexicana Hook.	+			2
8 MALVALES				
8.11 MALVACEAE				
Abelmoschus esculentus L. (Okra)	2			7
Abutilon indicum L.	+			5
Gossypium spp. (Cotton)	3		+	7, 2
Hibiscus mutabilis L.	+			14
Hibiscus panduraeformis Brum.	+			5
Hibiscus rosa-sinensis L.	1			14
Hibiscus vitifolius L.	+			10
Malachra capitata L.	+			9
Malvastrum coromandelianum (L.) Garcke	+			10
Malva rotundifolia L.	+			21
Sida acuta Brum.	+			5
Sida cordifolia L.	+			10
Sida spinosa L.	+			5
9 MALPIGHIALES				
9.12 LINACEAE				
Linum usitatissimum L. (Linseed)	2			24
10.13 EUPHORBIACEAE				
Acalypha lanceolata Willd.	+			5

Order, family, genus, and species of host plant	Species recorded			Reference*
	HA	HP	HAS	
Chrozophora rottleri (Geis) Sor.	+			10
Euphorbia hypericifolia L.	+			10
Phyllanthus maderaspatensis L.	+			10
Ricinus communis L. (Castor)	2			7
11 MYRTALES				
11.14 MYRTACEAE				
Eucalyptus sp.	+			10
12 RUTALES				
12.15 RUTACEAE				
Citrus aurantium L. (Sour lime)	+			7
Citrus limon (L.) Brum. (Lemon)	+			28
13 SAPINDALES				
13.16 SAPINDACEAE				
Cardiospermum halicacabum L.	+			5
13.17 ANACARDIACEAE				
Mangifera indica L. (Mango)	+			29
14 APOCYANALES				
14.18 ASCLEPIADACEAE				
Calotropis gigantea Dryand	+			5
15 RUBIALES				
15.19 RUBIACEAE				
Coffea arabica L. (Coffee)	+			14
16 BIGNONIALES				
16.20 PIDALIACEAE				
Martynia annua L.	+			5
Sesamum indicum L. (Sesame)	1			7
17 VERBENALES				
17.21 VERBENACEAE				
Lantana camara L.	+			5
18 PIPERALES				
18.22 PIPERACEAE				
Piper nigrum L. (Black pepper)	+			21
19 RHOEADALES				
19.23 PAPAVERACEAE				
Eschscholzia californica Cham.	+			21
Papaver somniferum L. (Opium)	+			7
20 BRASSICALES				
20.24 BRASSICACEAE				
Brassica oleracea L. (Cabbage)	1			32
Brassica nigra Koch (Mustard)	2			6
Raphanus spp.	+			21
21 CARYOPHYLLALES				
21.25 AIZOACEAE				
Trianthema sp.	+			10

Order, family, genus, and species of host plant	Species recorded			Reference*
	HA	HP	HAS	
22 CHENOPODIALES				
22.26 CHENOPODIACEAE				
Beta vulgaris L. (Beetroot)	+			9
Spinacia oleracea L. (Spinach)	1			21
22.27 AMARANTHACEAE				
Achyranthes aspera L.	+			5
Amaranthus gangeticus L.	+			1
Amaranthus paniculatus L.	+			5
Amaranthus polygamus L.	+			5
Digera muricata (L.) Mart.	+			5
Gomphrena celosioides Mart.	2			5
23 GENTIANALES				
23.28 GENTIANACEAE				
Centaurium sp.	+			5
24 PLANTAGINALES				
24.29 PLANTAGINACEAE				
Plantago lanceolata L.	+			21
25 SAXIFRAGALES				
25.30 SAXIFRAGACEAE				
Ribus ociculare SM.	+			9
26 UMBELLALES				
26.31 APIACEAE (UMBELLIFERACEAE)				
Coriandrum sativum L. (Coriander)	+			2
Daucus carota L. (Carrot)	+			14
27 ASTERALES				
27.32 ASTERACEAE (COMPOSITAE)				
Acanthospermum hispidum Dc. (Starburr)	1	3		18
Ageratum conyzoides L.	+			19
Althaea rosea L.	+			30
Calendula officinalis L.	+			14
Carthamus tinctorius L. (Safflower)	2	3		6
Chrysanthemum indicum L.	1			24
Chrysanthemum maximum L.	+			30
Chrysanthemum lecanthemum L.	1			24
Conzyna sp.	+			17
Cosmos bipinnatus Cuv.	+			5
Dahlia variabilis L.	+			30
Dianthus caryophyllus L.	+			30
Eclipta alba (L.) Hassk	+	2		5, 18
Emilia sonchifolia (L.) DC	+			4
Flaveria asutralasica Hook.	+			4
Gladiolus spp.	+			31
Grindelia camphorum Greene	+			21
Guizotia abyssinica Cass.	2			13
Helianthus annuus L. (Sunflower)	2			3
Laggera aurita L.	+			34

Order, family, genus, and species of host plant	Species recorded			Reference*
	HA	HP	HAS	
Lactuca sp. (Lettuce)	+			21
Melanthera aspera (Jacq.) L.C.	+			23
Parthenium hysterophorus L.	+			21
Picris echioides L.	+			14
Saussurea candidans Clarke.	+			10
Simsia grandiflora Benth.	+			5
Sonchus arvensis L.	+			5
Sonchus borealis	+			21
Sphaeranthus indicus L.	+			17
Taraxacum officinalis G.H. Weber	+			21
Tagetes erecta L.	+			13
Tagetes indica L.	+			12
Tridax procumbens L.	+			10
Vernonia cinera Less.	+			10
Zinnia elegans L.	+			30
28 SOLANALES				
28.33 SOLANACEAE				
Capsicum annuum L. (Chilli)	1			11
Datura fastuosa L.	+			35
Datura metel L.	1	+	2	5
Datura stramonium L.	+			9
Lycopersicon esculentum Mill. (Tomato)	3			7
Nicotiana rustica L.	+		2	7
Nicotiana tabacum L. (Tobacco)	1		3	24
Physalis minima L.	+		+	10
Physalis peruviana L.	+			2
Solanum melongena (Brinjal)	1			5
Solanum tuberosum L. (Potato)	1		1	2
Solanum xanthocarpum Sch. and Wendl.	+			5
28.34 CONVOLVULACEAE				
Ipomoea batata (L.) Lam. (Sweet potato)	1			8
29 PERSONALES				
29.35 SCROPHULARIACEAE				
Antirrhinum majus L. (Snapdragon)	+			27
Striga lutea Loureiro (Witchweed)	+			27
29.36 ACANTHACEAE				
Hygrophila agriculata (K. Sdhum) Heine	+			10
30 GERANIALES				
30.37 GERANIACEAE				
Erodium moschatum L. Her.	+			21
Geranium carolinianum Crantz.	+			21
31 POLEMONIALES				
31.38 POLEMONIACEAE				
Phlox drummondii Hook.	+			10
32 BORAGINALES				
32.39 BORAGINACEAE				
Heliotropium scabrum Retz.	+			10

Order, family, genus, and species of host plant	Species recorded			Reference*
	HA	HP	HAS	
33 LAMIALES				
33.40 LAMINACEAE (LABIATAE)				
Leucas aspera Spreng.	+			5
Mentha spicata L. Hudson. (Spearmint)	+			25
Ocimum sp.	+	+		10
MONOCOTYLEDONS				
34 COMMELINALES				
34.41 COMMELINACEAE				
Commelina benghalensis L.	+			5
35 ZINGIBERALES				
35.42 MUSACEAE				
Musa sp.	+			14
36 LILIALES				
36.43 LILIACEAE				
Allium cepa L.k. (Onion)	+			8
37 AMARYLLIDIALES				
37.44 AMARYLLIDACEAE				
Polianthus tuberosa L.	+			12
38 GRAMINALES				
38.45 POAICEAE (GRAMINEAE)				
Avena sativa L. (Oats)	1			8
Eleusine coracana (L.) Gaertn. (Finger millet)	1			9
Pennisetum americanum (L.) Leeke (Pearl millet)	3			7
Oryza sativa L. (Rice)	+			15
Setaria italica Beauv. (Foxtail millet)	1			10
Sorghum bicolor (L.) Moench (Sorghum)	3			11
Triticum aestivum L. (Wheat)	1			19
Zea mays L. (Maize)	2			11

*Numbers indicate references to authors: 1. Abdul Kareem, et al. 1970, 2. Achan, et al. 1968, 3. Ayyar 1940, 4. Ballard 1921, 5. Bhatnagar & Davies 1978, 6. CIBC 1968, 7. Fletcher 1917, 8. Fletcher 1920, 9. Fletcher 1921, 10. ICRISAT 1974–85, 11. Katagihallimath 1963, 12. Manjunath 1972, 13. Manjunath, et al. 1970, 14. Mathur 1942, 15. Nayar, et al., 16. Patel & Patitundu 1981, 17. Patel, et al. 1964, 18. Patel, et al. 1971, 19. Patel, et al. 1973, 20. Pruthi & Batra 1960, 21. Puttarudriah 1953, 22. Rai & Nagesh Chandra 1972, 23. Rajagopal & Channa Basavanna 1975, 24. Rao 1968, 25. Reddy 1973, 26. Reed & Pawar 1982, 27. Sankaran & Rao 1968, 28. Sharma, et al. 1970, 29. Siddappaji 1972, 30. Singh 1983, 31. Sivagami & David 1968, 32. Srivastava & Saxena 1958, 33. Subbarao, et al. 1974, 34. Wardeikar & Kausale 1980.

Host Plants of *H. Armigera*

H. armigera has been recorded feeding on 181 cultivated and uncultivated plant species belonging to 45 families—40 dicots and 5 monocots (see Table 2). While the number of plant species in different families could be indicative of the plant characters attractive to *H. armigera*, the 22 plant

species that we have adjudged as important hosts belong to the families Amaranthaceae, Asteraceae (Compositae), Brassicaceae, Capparidaceae, Euphorbiaceae, Fabaceae (Leguminosae), Linaceae, Malvaceae, Poaiceae (Gramineae), and Solanaceae. Nevertheless, some of the 160 plant species which have been considered here as being of minor or doubtful importance have been observed at times sustaining high populations of *H. armigera*.

Based on present estimates, current economic damage due to *H. armigera* largely occurs in pigeonpea, *Cajanus cajan* L.; chickpea, *Cicer arietinum* L.; tomato, *Lycopersicon esculentum* L.; and cotton, *Gossypium* spp. However, many other crops—including sorghum, *Sorghum bicolor* (L.) Moench; pearl millet, *Pennisetum americanum* (L.) Leeke; maize, *Zea mays* L.; groundnut, *Arachis hypogaea* L.; and okra, *Abelmoschus esculentus* L.—are fed upon, and estimates would reveal damage here also.

On legumes

H. armigera is the most important pest on legumes throughout India. In central and southern India, it is best known as the "pod borer" of pigeonpea (Figure 2a). Seshu Reddy and Channa Basavanna (1978) established that an average infestation of one larva per plant of pigeonpea can cause a yield loss of 1025 kg/ha. Bhatnagar et al. (1982) who assessed the pigeonpea pod damage during 1975–81 in 1297 farmers' fields spread across the major pigeonpea-producing areas of the country, reported damage due to lepidopteran larvae as 29.7% in the northwest zone, 13.2% in the north zone, 24.3% in the central zone, and 36.4% in the south zone. *H. armigera* was the major pest. Similar studies conducted by Bhatnagar et al. (1982) on chickpea (Figure 2b) revealed that 7.5% of pods, on an average, were damaged by *H. armigera*. These could be underestimates, for there can be substantial loss due to vegetative and floral feeding, which is difficult to assess. The combined losses caused by *H. armigera* on pigeonpea and chickpea in India have been estimated to exceed U.S. $300 million in some years (Reed and Pawar 1982). On groundnut, where *H. armigera* is a foliage feeder, it does not cause economic damage at present levels of infestation (Pawar et al. 1985).

On cotton

Earlier in the century, *H. armigera* was not regarded as a major pest of cotton in India. Lefroy (1906), at the time when this species was wrongly thought to be synonymous with *H. zea* (Boddie), wrote, "In America the insect attacks the bolls of cotton, a habit never recorded against it in India." Similarly, Fletcher (1914) did not mention cotton when he listed the host plants of this insect in southern India. However, the situation has changed since then; *H. armigera* is now regarded as one of the serious pests of cotton (Figure 2c) in several parts of India, but with great variability in its attack over areas and seasons. For example, Kaushik et al. (1969)

a) Pigeonpea

b) Chickpea
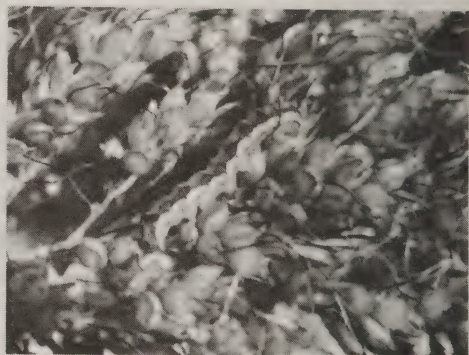
c) Cotton

d) Sorghum
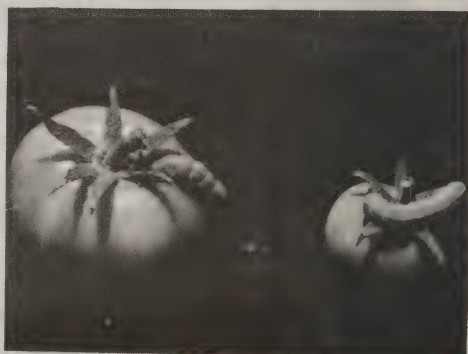
e) Pearl millet

f) Tomato

Figure 2. *Heliothis armigera* larvae feeding on some important crop hosts: a—Pigeonpea; b—Chickpea; c—Cotton; d—Sorghum; e—Pearl millet; f—Tomato.

reported losses of 41–56% in Madhya Pradesh, and Manjunath (1974) up to 14% in Anand, Gujarat, but Nair (1975) considered it only a minor pest.

On cereals

In central and southern India, *H. armigera* sometimes occurs in considerable populations on sorghum (Figure 2d) and pearl millet (Figure 2e). In sorghum, yield losses up to 37.1% have been reported (Kulkarni et al. 1980); however, it is not yet regarded as a major pest of these crops. On maize, large numbers of eggs are often seen on silk in the cob, although the larval population generally remains low. *H. armigera* causes no economic damage in these crops, largely because of high parasitism of its eggs and early-instar larvae (Manjunath et al. 1970; Bhatnagar et al. 1983; Pawar et al. 1985).

On tomato

H. armigera is generally referred to as the "fruit borer" on tomato (Figure 2f), which is heavily damaged in different parts of the country (CIBC 1974). It is reported to have damaged 40–50% of the fruits in Tamil Nadu (Srinivasan 1959) and 60–70% in Karnataka (Manjunath et al. 1970).

The wide host range of *H. armigera* ensures that there is a continuous availability of host plants for larvae to feed on throughout the year. The period of appearance, peak population, and declining activity of this pest throughout the year on important host plants in Bangalore (Karnataka) are shown in Figure 3. The larvae were most abundant from September to November.

In Andhra Pradesh, the larvae were found on irrigated tomatoes and other vegetables, and on a few wild hosts during the hot dry season (March–June). Soon after the onset of rains, populations build up on groundnut, sorghum, and pearl millet (July–October). Very large populations are found on pigeonpea and chickpea from November to March (Bhatnagar et al. 1982).

In northern India, populations of *H. armigera* are at a peak on chickpea in April and on cotton in September and October. The pest is reported to survive the cold winters as diapausing pupae (Lal 1983).

Host Plants of *H. assulta*

H. assulta has a very narrow host range. Five of the seven recorded host plants belong to the family Solanaceae (see Table 2). Although there is an old report (Fletcher 1914) of its occurrence on chickpea (Fabaceae or Leguminosae) and cotton (Malvaceae), the similarity of larvae and moths of *H. assulta* and *H. armigera* may have resulted in misidentification.

The weed *Datura metel* is the most preferred host of *H. assulta*. Studies

210
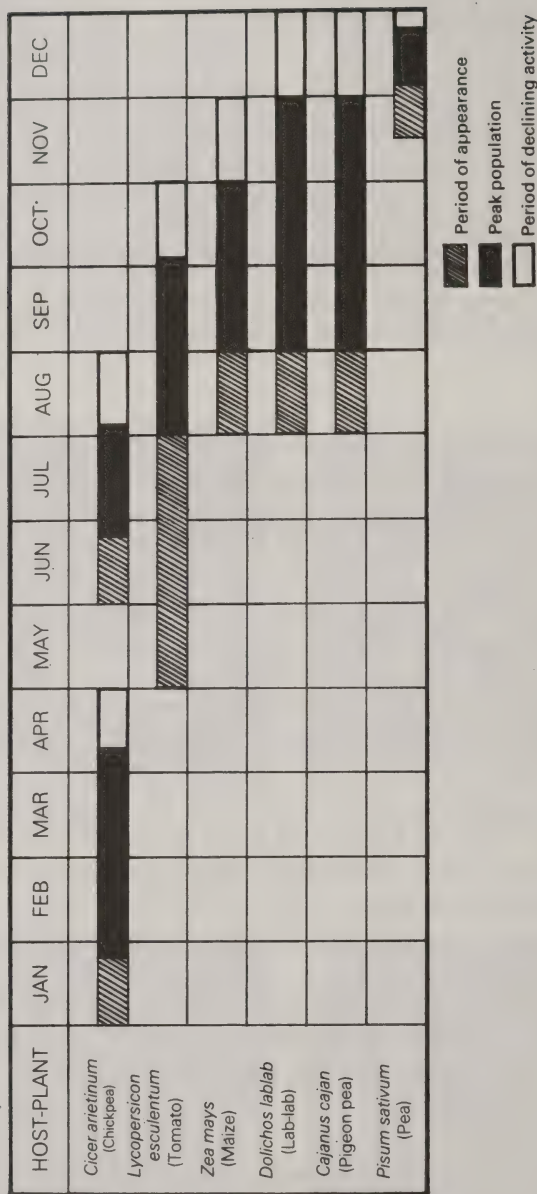
Figure 3. Period of activity of *Heliothis armigera* on its important hosts at Bangalore, Karnataka state, India.

conducted at Patancheru (Andhra Pradesh) on the relative population of *Heliothis* spp. on this weed revealed that 86.5% were comprised of *H. assulta,* 13.1% of *H. armigera,* and 0.4% of *H. peltigera* (Bhatnagar and Davies 1978). Larvae were available throughout the year.

The extent of damage to tobacco by *H. assulta* has not yet been assessed but is generally low.

Host Plants of *H. peltigera*

H. peltigera has been reported from only seven host plants belonging to five families. It mainly feeds on wasteland weeds such as *Acanthospermum hispidum* and has also been reported as a pest of safflower, *Carthamus tinctorius.*

Pawar et al. (in press) reported that *H. peltigera* was predominant (72.8%) in sole-cropped safflower, where *H. armigera* was only 27.2%. However, on intercropped safflower in general, *H. armigera* populations were slightly higher (51.9%) than *H. peltigera* (48.5%), the proportion being governed largely by the presence of companion crops; for instance, chickpea and cowpea companion crops attracted *H. armigera* on safflower.

Manjunath et al. (1976) found that *H. peltigera* markedly preferred *A. hispidum* for oviposition and larval feeding; they reported that it did not cause economic damage to any crop around Anand, in Gujarat state. Studies conducted at Patancheru revealed that 93.9% of the *Heliothis* populations on *A. hispidum* were comprised of *H. peltigera,* while 6.1% were *H. armigera.*

PARASITOIDS AND PREDATORS OF *HELIOTHIS* SPP. IN INDIA

A large number of parasitoids and predators have been recorded on *Heliothis* spp. in India. Pathogens are also known, but not dealt with in this paper.

Parasitoids

A consolidated list of parasitoids of *H. armigera, H. assulta,* and *H. peltigera* is presented in Table 3 and summarized below.

Parasitoid	No. of parasitoid species from			Total parasitoid species[1]
	H. armigera	*H. assulta*	*H. peltigera*	
DIPTERA				
Sarcophagidae	1	—	—	1
Tachinidae	26	4	6	27
Chloropidae	1	—	—	1

HYMENOPTERA

Bethylidae	1	—	—	1
Braconidae	18	6	3	21
Chalcididae	2	—	—	2
Eulophidae	1	—	—	1
Ichneumonidae	17	2	4	19
Scelionidae	1	—	—	1
Trichogrammatidae	7	—	2	8

NEMATODA

Mermithidae	2	1	1	2
Total	77	13	16	84

Table 3. Parasites of Heliothis *spp. reported in India*

	Host stage	
HA : *Heliothis armigera*	e: Egg	lp: Larval-pupal
HP : *Heliothis peltigera*	el: Egg-larval	p: Pupal
HAS : *Heliothis assulta*	l: Larval	

Parasitoid	Host stage parasitized	*Heliothis* spp. parasitized			Reference*
		HA	HP	HAS	
INSECTA					
DIPTERA					
SARCOPHAGIDAE					
Sarcophaga orientoides S.W.	l	+			6
TACHINIDAE					
Carcelia sp.	lp	+	+		1
Carcelia (Stenometopia) illota Curran	lp	+	+	+	1, 18
Carcelia kolkiana Townsend	lp	+			1
Carcelia raoi Mesnil	lp	+			19
Carcelia peraequalis Mesnil	lp	+			1
Compsilura concinnata Meigen	l	+			6
Drino (Prosturmia) imberbis Wiedemann	l	+			1
Drino sp. nr. *unisetosa* Bar.	l	+			1
Eucelatoria bryani Sabrosky**	l	+			5
Exorista fallax Meigen	l	+			1
Exorista japonica Townsend	l	+			1
Exorista xanthaspis Wiedemann	l	+			19
Goniophthalmus halli Mesnil	lp	+	+	+	1, 19
Isomera cinerascens Rondani	l	+			1
Pales coeruleo-nigra Mesnil	l	+			6
Palexorista sp.	l	+	+		9
Palexorista laxa Curran	l	+	+		16, 13
Palexorista solennis Walker	l	+		+	16
Sisyropa apicata Bar.	l	+			1
Spallanzania sp.	l			+	1

Parasitoid	Host stage parasitized	*Heliothis* spp. parasitized			Reference*
		HA	HP	HAS	
Strobliomyia aegyptia Vill.	l	+			1
Sturmiopsis inferens Townsend	l	+	+		16
Suensonomyia n. sp.	l	+			1
Thecocarcelia incedens Rondani	l	+			1
Voria edentata Bar.	l	+			1
Voria ruralis Fallen	l	+			1
Winthemia sp. nr? *diversoides* Bar.	l	+			1
CHLOROPIDAE					
Mepachymerus ensifer Thompson	l	+			22
HYMENOPTERA					
BETHYLIDAE					
Goniozus sp.	l	+			20
BRACONIDAE					
Apanteles sp.	l	+		+	1
Apanteles sp. (*glomeratus* group)	l		+		1
Apanteles sp. nr. *glomeratus* L.	l	+			1
Apanteles ruficrus Haliday	l	+			1
Bracon sp.	l	+		+	1
Bracon brevicornis Wesmael	l	+			1
Bracon cushmani Muesbeck	l	+			6
Bracon gelechiae Ashmead	l	+			1
Bracon greeni Ashmead	l	+			1
Bracon hebetor Say	l	+			6
Chelonus sp.	el	+			9
Chelonus heliopae Gupta	el	+	+		1, 17
Chelonus narayani Subba Rao	el	+			21
Microchelonus curvimaculatus Cameron	el	+	+	+	9
Microplitis maculipennis (Szepligeti)	l	+			10
Microplitis sp.	l	+			8
Microplitis sp. nr. *pallidipes* Szepligeti	l			+	1
Odentepyris sp.	l	+			1
Paraphylax sp.	l	+			6
Rogas sp.	l	+		+	1
Rogas sp. ? *testaceus* Spinola	l			+	1
CHALCIDIDAE					
Brachymeria responsator Walker	p	+			1, 19
Tetrastichus ayyari Rohwer	p	+			4
EULOPHIDAE					
Euplectrus spp.	l	+			15
Ichneumonidae					
Agrypon nox Morley	l	+			15

Parasitoid	Host stage parasitized	Heliothis spp. parasitized			Reference*
		HA	HP	HAS	
Attractodes sp.	1	+			15
Banchopsis ruficornis Cameron	1	+			8
Barichneumon sp.	1	+			14
Campoletis chlorideae Uchida	1	+	+	+	9
Campoletis maculipes (Tsch.)	1		+		16, 13
Campoletis (Ecphoropsis) sp.	1	+			11
Disophrys sp.	1	+			9
Enicospilus sp.	1	+			1
Enicospilus sp. nr. *shinkanus* Uchida	1	+			18
Eriborus argenteopilosus Cameron	1	+	+		1, 9
Eriborus pilosellus Cameron	1	+			1, 19
Eriborus trochanteratus Morley	1	+			3
Ichneumon sp.	1	+			3
Metopius rufus Cameron	1	+			3
Netelia sp.	1	+		+	1, 15
Pristomerus sp.	1		+		17
Temelucha sp.	1	+			3
Xanthopimpla stemmator Thunberg	lp	+			3
SCELIONIDAE					
Telenomus sp.	e	+			11
TRICHOGRAMMATIDAE					
Trichogramma sp.	e	+			3
Trichogramma achaeae Nagaraja & Nagarkatti	e	+			12
Trichogramma brasiliensis Ashmead*	e	+			5
Trichogramma chilonis Ishii	e	+	+		12, 9
Trichogramma chilotraeae Nagaraja	e		+		12
Trichogrammatoidea sp.	e	+			3
Trichogrammatoidea armigera Nagaraja	e	+			11
Trichogrammatoidea bactrae sp. *fumata* Nagaraja	e	+			3
NEMATODA					
MERMITHIDAE					
Hexamermis sp.	1	+			1
Ovomermis albicans (Siebold)	1	+	+	+	2

*Numbers indicate reference to authors: 1. Achan, et al. 1968, 2. Bhatnagar & Davies 1978, 3. Bhatnagar, et al. 1982, 4. Cherian & Subramaniam 1940, 5. CIBC 1968, 6. CIBC 1974, 7. Gangrade 1963, 8. Hussain & Mathur 1924, 9. ICRISAT 1974-85, 10. Krishnamurthy & Usman 1954, 11. Manjunath 1972, 12. Manjunath, et al. 1970, 13. Manjunath, et al. 1976, 14. Mathur 1967, 15. Mathur 1970, 16. Patel & Patitundu 1981, 17. Patel, et al. 1971, 18. Pawar, et al. 1985, 19. Rao 1968, 20. Sivagami, et al. 1975, 21. Subba Rao 1955, 22. Verma, et al. 1971.

**Imported parasitoids; field recovery reported.

Altogether 77 parasitoids of *H. armigera,* 13 on *H. assulta,* and 16 on *H. peltigera* have been reported from India. Included in the list are two exotic parasitoids, *Trichogramma brasiliensis* (Trichogrammatidae) and *Eucelatoria bryani* (Tachinidae), earlier misidentified as *E. armigera,* which have been recovered from *H. armigera* following their field releases in Bangalore (CIBC 1968; Pawar et al. 1981; Mani and Krishna Murthy 1983). Some important parasitoids are illustrated in Figure 4.

Egg parasitism

Seven species of trichogrammatids and one scelionid have been recorded as egg parasitoids of *H. armigera;* two trichogrammatids also parasitized *H. peltigera.* Parasitism by trichogrammatids is much influenced by host plants. More eggs are often laid on marigold, *Tagetes erecta* L., and tuberose, *Polianthes tuberosa* L., when they are in full bloom, and on maize when cobs are silking. Such *Heliothis* eggs were found heavily parasitized (up to 85%), predominantly by *Trichogramma chilonis* Ishii (previously misidentified, first as *T. australicum* Girault and later as *T. confusum* Viggiani). Thus only a few larvae were found on these plants (Manjunath et al. 1970). The possibility of using marigold and such plants as trap crops may be worth examining. Up to 80% of the eggs laid on tomato and 20% on niger, *Guizotia abyssinica* Cass., were recorded parasitized by *Trichogramma* (Manjunath 1972).

Studies conducted in Gujarat showed that *H. armigera* eggs collected from tomato, potato, and lucerne fields were heavily parasitized by *T. chilonis,* up to 98.2% in 1973–74 and 84.2% in 1974–75. However, no parasitism was recorded in eggs collected from chickpea; an acidic exudate of the plants was thought to be a deterrent to the parasitoid (Yadav 1980; Yadav and Patel 1981).

Bhatnagar et al. (1982) observed that of nearly 12,000 eggs of *H. armigera* collected from sorghum from August to October, 1978–80, 26.4% were parasitized by *Trichogramma,* but of more than 9,000 eggs collected from pigeonpea from September to February, 1978–81, in the same fields, only 0.1% were parasitized. While the eggs on chickpea were free from parasitism, those on other crops—including cowpea, mung bean, groundnut, maize, sorghum, pearl millet, and cotton—revealed parasitism ranging up to 85%. The absence of parasitism on chickpea and the almost negligible parasitism on pigeonpea is an important factor in the high population buildup of *Heliothis* on these crops.

More recent work at ICRISAT has shown that different host plants affect parasitism by *T. chilonis* in no-choice situations (Singh and Sithanantham, in press) and these influences seem to differ with the plant part of the host (Sithanantham et al. 1982).

Figure 4. Some important natural enemies of *Heliothis* spp. in India: a—*Campoletis chlorideae*; b—*Enicospilus* sp.; c—*Carcelia illota*; d—*Delta pyriforme*; e—*Delta* sp. mud nest, showing *Heliothis* larvae; f—Nematode *Ovomermis albicans*.

a) *Campoletis chlorideae*

b) *Enicospilus* sp.
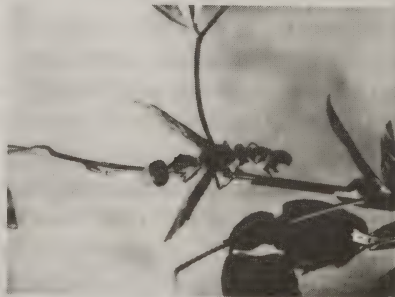
c) *Carcelia illota*

d) *Delta pyriforme*

e) *Heliothis* larvae in mud-nest of *Delta* sp.

f) Nematode, *Ovomermis albicans*

The weed *A. hispidum* is the most preferred host of *H. peltigera* for oviposition and feeding. In Anand, Gujarat, *H. peltigera* was effectively suppressed by the egg parasitoid, *Trichogramma chilotraeae* Nagaraja and Nagarkatti, which often parasitized more than 50% of the eggs and occasionally up to 100% (Manjunath et al. 1976).

Larval parasitism

Larval parasitoids attack young to mature larvae, and a few are also egg-larval or larval-pupal parasitoids. Of the large number of parasitoids recorded on *H. armigera, Campoletis chlorideae* Uchida (Figure 4a)— earlier misidentified as *Ecphoropsis perdistinctus* Viereck—*Eriborus* sp. (Hym., Ichneumonidae), *Carcelia illota* (Curran) (Figure 4c), *Goniophthalmus halli* Mesnil, and *Palexorista laxa* Curran (Dipt., Tachinidae) were most common. *C. chlorideae* and *C. illota* were most active on several crops and also across seasons. Some information on the extent of parasitism by various species on different host plants and in different seasons is given by Achan et al. (1968), CIBC (1974), Bhatnagar et al. (1983), and Pawar et al. (1985). In general, the hymenopterans attacked small larvae, and the dipterans parasitized large larvae.

There are considerable host-plant influences on the species and magnitude of parasitism (CIBC 1974). Bhatnagar et al. (1982) reported that the hymenopterans were predominant on sorghum and dipterans were predominant on pigeonpea. The extent of parasitism of *H. armigera* larvae on sorghum by dipterans was only 2.1%, while it was up to 24.9% by hymenopterans. Similarly, there was considerable difference in the parasitism levels and parasitoid species attacking *Heliothis* larvae infesting pigeonpea and chickpea, even when these were grown in the same areas and infested at the same time. On *H. armigera* infesting pigeonpea, parasitism by dipterans was up to 22%; by hymenopterans, 5%. On *H. armigera* infesting chickpea, parasitism was 3% by dipterans and 17.2% by hymenopterans. Thus, hymenopterans preferred larvae on chickpea, while the dipterans preferred those on pigeonpea (Bhatnagar et al. 1983).

Hyperparasitism of *Heliothis* parasitoids has been reported. Cocoons of *C. chlorideae* were reported parasitized by chalcids *Brachymeria* sp., *B.* sp. nr. *apantelesi* Risbec, *B. excarinata* Gahan, *B.* sp. nr. *persica* Masi, and *B. wittei* (Schmitz); the eulophid *Nesolynx javanica* (Ferr); the eurytomids *Aximopsis* sp. and *Eurytoma* sp.; the ichneumonid *Hemiteles* sp.; and *Pteromalus* sp. (Achan et al. 1968, Bhatnagar et al. 1983). However, hyperparasitism generally remained low.

Nematodes were reported most active during the rainy season. In Bangalore, *Hexamermis* sp. were reared from over 40% of the *H. armigera* larvae collected from tomato during September–November (CIBC 1974).

Bhatnagar et al. (1985) recovered *Ovomermis albicans* (Figure 4f) from all three species of *Heliothis* infesting various crops and weeds in Andhra Pradesh. The nematode was more active in light soils (Alfisols) than in heavy soils (Vertisols), and the incidence of occurrence was higher on low-growing crops like groundnut and tomato and weeds. The levels of parasitism on *H. armigera* larvae, over the years, on some important crops were: 3.8–39.4% on groundnut, 42.5–52% on tomato, 0.7–2.9% on sorghum, and 2–2.4% on pigeonpea. Parasitism on *H. peltigera* on *A. hispidum* was 1.3–46.1%; that on *H. assulta* on *Datura metel*, 0.4–4%.

Predators

Altogether, 33 predators have been reported from *Heliothis* spp. in India (Table 4). The wasps *Delta* spp. (Figure 4d) have been observed to paralyze *H. armigera* larvae to place in the cells of their mud nests before oviposition, even carrying the larvae from distant fields. As many as 14 *Heliothis*

Table 4. Predators of Heliothis *spp. reported in India.*

Predator	Heliothis spp. attacked			Reference*
	HA	HP	HAS	
INSECTA				
DERMAPTERA				
CARCINOPHORIDAE				
Euborellia annulipes (Lucas)	+			1
Euborellia stali Dohrn	+			1
LABIDURIDAE				
Nala lividipes (Dufour)	+			1
DICTYOPTERA				
MANTIDAE				
Humbertiella sp.	+			1
HEMIPTERA				
REDUVIIDAE				
Catamiarus brevipennis (Serv.)	+			1
Coranus spinicutis Reut.	+			2
Ectrychotes dispar Reut.	+			1
Oncocephalus annulipes Stål.	+			2
Rhinocoris fuscipes Stål.	+			2
Rhinocoris marginatus (F.)	+			1
Sycanus indagator Stål.	+			2
LYGAEIDAE				
Paromius gracilis (Rambur)	+			1
PENTATOMIDAE				
Cantheconidea furcellata (Wolff.)	+			1

Predator	Heliothis spp. attacked			Reference*
	HA	HP	HAS	
NABIDAE				
Tropiconabis capsiformis (Germar)	+			1
ANTHOCORIDAE				
Orius maxidentex Ghauri	+			1
HYMENOPTERA				
EUMENIDAE				
Delta companiforme esuriens F.	+			5
Delta conoideum (Gmelin)	+			5
Delta pyriforme (F.)	+			5
FORMICIDAE				
Cataglypsis bicolor F.	+			3
Camponotus sericeus F.	+	+		4
SPHECIDAE				
Sphex argentatus F.	+			1
VESPIDAE				
Polistes olivaceus Degeer	+			1
Repalidia marginata Lepeltier	+			1
Vespa orientalis F.	+			1
Vespa tropica haemotodes Bequaert	+			1
NEUROPTERA				
CHRYSOPIDAE				
Chrysopa carnea Stephen	+	+		4
Chrysopa sp.	+			1
COLEOPTERA				
COCCINELLIDAE				
Menochilus sexmaculatus F.	+			1
ACARINA				
ARANEIDA				
THOMISIDAE				
Oxyptila reenae (Basu)	+			1
Thomisus sp.	+			1
CLUBIONIDAE				
Clubiona sp.	+			1
ARANIDAE				
Neoseona theis (Walck.)	+			1
Leucauge tessellata (Thorb.)	+			1

*Numbers indicate reference to authors: 1. Bhatnagar et al. 1983, 2. CIBC 1974, 3. Khan & Sharma 1972, 4. Manjunath et al. 1970, 5. Pawar & Jadhav 1983.

larvae were recorded in a cell (Figure 4e). *Chrysopa,* a general predator, also preys upon eggs and small larvae of *Heliothis,* particularly on sunflower and cotton. However, the role of predators in regulating *Heliothis* populations has not yet been quantified.

FACTORS AFFECTING ACTIVITY OF NATURAL ENEMIES

Cropping Systems

It has been observed that the parasitoids which build up populations on one crop do not necessarily move to another crop where infestation by the same species of *Heliothis* may be prevalent. For example, in sorghum/pigeonpea intercrops in the Indian subcontinent, sorghum matures and is harvested before pigeonpea flowers. Eggs and larvae of *H. armigera* are common on sorghum heads and are heavily parasitized by hymenopterans, notably by *T. chilonis* and *C. chlorideae*. Although these parasitoids build up in high populations on sorghum, they give little advantage to the companion pigeonpea, as they do not subsequently move to and parasitize *Heliothis* on the second crop. Similarly, the activity of tachinids in sorghum is very low, but they are the major parasitoids of *H. armigera* on pigeonpea. A simplified diagrammatic representation of parasite move-
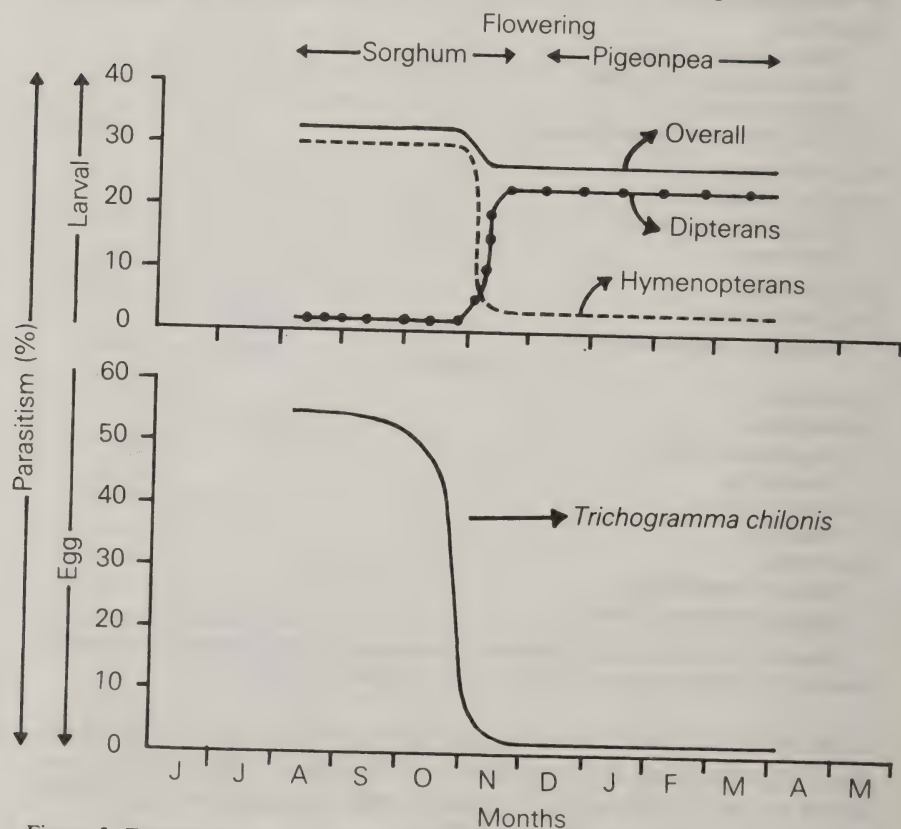
Figure 5. Transfer of parasitoids of *Heliothis armigera* in a cereal/pulse intercrop at Patancheru, Andhra Pradesh, India (simplified diagrammatic representation) (Source: Bhatnagar and Davies 1979.)

ment in sorghum/pigeonpea (after Bhatnagar and Davies 1979) is given in Figure 5.

Pawar et al. (in press) reported differences in both the parasitoid complex and the level of parasitism between sole crop and intercrop and also among intercrops of safflower. The parasitoids *Microchelonus curvimaculatus* Cameron (Hym., Braconidae) and *Palexorista solennis* Walker (Dipt., Tachinidae) were recovered from *H. armigera* on some intercrops but not from *H. armigera* on sole-cropped safflower.

Some differences have been observed in preferences of wasps *Delta* spp. in preying on *Heliothis* larvae from different crops.

Weeds

Weeds contributed to the maintenance of the resident *Heliothis* population as well as to that of certain important parasitoids in the absence of crops. Parasitic nematodes and *C. chlorideae* parasitize *Heliothis* larvae in significant numbers on weeds during the off-season and towards the beginning of the season, before the surviving populations in subsequent generations become a threat to the main crops. The levels of parasitism of *Heliothis* spp. on various weeds in Andhra Pradesh have been reported by Bhatnagar et al. (1983, 1985).

Acanthospermum hispidum supports activity of parasitoids on *H. peltigera*. In Anand, Gujarat, egg parasitism by *T. chilotreae* up to 100% and larval parasitism up to 26.7%, principally by *Campoletis maculipes* (Tsch.), has been recorded on this weed (Manjunath et al. 1976).

Type of Soil

Pawar et al. (1984) recorded higher parasitism of *H. armigera* on sorghum grown on Alfisols than Vertisols. Wasps *Delta* spp. were also reported more active on Alfisols than Vertisols (Pawar and Jadhav 1983).

CONCLUSIONS

1. Of the three species of *Heliothis* that occur in India, only *H. armigera* is currently of great economic importance. *H. assulta and H. peltigera* are mostly restricted to weeds, notably *Datura metel* and *Acanthospermum hispidum,* respectively.

2. Of the 181 plant species recorded as hosts of *H. armigera,* only 21 species are important. Presently, pigeonpea, chickpea, tomato, and cotton suffer economic damage, and some crops, including sorghum, pearl millet, maize, tobacco, and lucerne, probably receive damage, but this damage has not been estimated.

3. Seventy-seven parasitoids have been recorded on *H. armigera,* 13 on *H. assulta,* and 16 on *H. peltigera* in India. The most important

parasitoids of *H. armigera* are the hymenopterans—*Campoletis chlorideae, Eriborus* sp., and *Trichogramma chilonis*; the dipterans—*Carcelia illota, Goniophthalmus halli* and *Palexorista laxa*; and the nematodes—*Ovomermis albicans* and *Hexamermis* sp.

4. There is considerable crop influence on the activity of parasitoids. In general, the hymenopteran larval parasitoids are more active in cereal crops and the dipterans are more prevalent in legumes, particularly pigeonpea. Egg parasitism by *Trichogramma* was highest on cereals, tomato, and several other crops but negligible on chickpea and pigeonpea.

5. Altogether, 33 predators have been reported from *Heliothis* spp., but their impact on pest suppression has not been assessed.

6. Detailed studies on the bioecology of parasitoids and predators, with particular reference to the insect host, host plant, and season, are required to exploit the natural enemies of *Heliothis* in its management. We need greater understanding in this context of the influence of host plants on natural enemies. Since different stages of the pest are attacked by promising parasitoids—eggs by *Trichogramma*; early-instar larvae by *C. chlorideae, Eriborus* sp, and *Apanteles* sp; and late-instar larvae by the tachinids and nematodes—sequential releases of these parasitoids might by helpful in tackling this major pest.

Acknowledgments

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Distribution and Economic Importance of *Heliothis* spp. in Pakistan and Their Natural Enemies and Host Plants

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ABSTRACT

Two species of the genus *Heliothis* Ochsenheimer, *H. armigera armigera* (Hübner) and *H. assulta assulta* Guenée have been reported from Pakistan. *H. armigera* is a serious pest of a number of crops but almost no work has been done on its biology, ecology, host plants, and natural enemies.

In Pakistan, it has been reported from 40 plant species, ranging from 20 to 2500 m altitude, and occurring in a variety of climatic conditions. Eight species of parasites recorded from *Heliothis* include *Campoletis chlorideae* Uchida, *Enicospilus* sp., *Netelia ocellaris* (Thomson), *Apanteles* sp., *Bracon hebetor* Say, *Trichogramma chilonis* Ishii, *Exorista xanthaspis* Wiedemann, and *Palexorista* sp. Some 16 species of parasites from other countries have been recommended for introduction into Pakistan.

Two species of the genus *Heliothis* Ochsenheimer—*H. armigera* (Hübner) and *H. assulta assulta* (Guenée)—have been reported from Pakistan (Hardwick 1965). However, parasites have been reported only from *H. armigera,* most probably because *H. assulta assulta* has been confused with *H. armigera.* In Pakistan, *H. armigera* is a serious pest of a number of crops such as cotton, tobacco, sugarbeet, maize, potato, tomato, pulses, etc. However, in spite of its great economic importance, almost no work has been done on its biology, ecology, host plants, and natural enemies.

A project has been started under the PL-480 program for a country-wide survey for different species/strains of *Heliothis* spp., their host plants, and distribution, and for studies on their biology, status, natural enemies, and mating compatibility among different species/strains.

In this paper, distribution, host plants, and parasites that have been recorded in Pakistan and possibilities of introduction from other areas are discussed.

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DISTRIBUTION AND PHENOLOGY

In Pakistan, *H. armigera* has been recorded from the coast (altitude 20 m) to the mountains (2500 m), occurring in a variety of climatic conditions ranging from a temperate climate in the mountains, with snow during winter, to subtropical and tropical in the foothills, plains, and coastal areas. There is considerable variation in precipitation, from high rainfall in the north to arid conditions in the south.

The phenology of *H. armigera* and number of generations per year have not been studied. Meng et al. (1962) suggested that in China this species has three generations a year north of 40° N, four between 30° and 40° N, five between 25° and 30° N, and six south of 25° N. If this criterion is applied in Pakistan, it may have up to six generations in the south, four in the north, and perhaps one or two at high altitudes.

H. assulta has been reported from Allahabad (Hardwick 1965); no other information is available on this species in Pakistan.

HOST PLANTS

In Pakistan, *H. armigera* larvae have been recorded feeding on 40 plant species belonging to 19 families (CIBC 1969) which include crops, weeds, and ornamentals (Table 1). There must be many more host plants, because in India, Bhatnagar and Davies (1978) reported this pest feeding on 105 species in Andhra Pradesh and neighboring states.

Table 1. Plant species recorded as hosts of Heliothis armigera *in Pakistan*

Family	Species	Distribution
Gramineae	*Saccharum officinarum* L.	Hafizabad
	Triticum aestivum L.	Murree
	Zea mays L.	Rawalpindi & Hyderabad
Cannabinaceae	*Cannabis sativa* L.	Balakot
Loranthaceae	*Dendrophthoe falcata* (Linn.) Etting	Kahuta
Polygonaceae	*Rumex chalepensis* Miller	Dir
Chenopodiaceae	*Beta vulgaris* L.	Malakand, Bahawalpur & Peshawar
Cruciferae	*Brassica campestris* L.	Rawalpindi
	Coronopus didymus (L.) Smith	Dir
Rosaceae	*Crataegus songarica* Koch C.	Barawal Bandi (Dir)
	Rosa sp.	Peshawar

Family	Species	Distribution
Papilionaceae	*Astragalus* sp.	Dir
	Cicer arietinum L.	Rawalpindi, Faisalabad & Latamber (D.I. Khan)
	Lathyrus odoratus L.	Peshawar
	Lens culinaris Medicus	Likora
	Pisum sativum L.	Timurgarha
	Trifolium alexandrinum L.	Haripur
	T. resupinatum L.	Malakand & Peshawar
Geraniaceae	*Geranium* sp.	Timurgarha & Peshawar
Euphorbiaceae	*Chrozophora hierosolymitana* Sprengel	Dir
Malvaceae	*Abelmoschus esculentus* (L.) Moench	Peshawar & Bahawalpur
	Althaea rosea (L.) Cavanilles	Peshawar & Chakdara
	Gossypium herbaceum L.	Rawalpindi & Multan
Hypericaceae	*Hypericum perforatum* L.	Rawalakot
Umbelliferae	*Foeniculum vulgare* Miller	Charsadda
Oleaceae	*Jasminum* sp.	Timurgarha
Boraginaceae	*Trichodesma indicum* (L.) R. Br.	Rawalpindi
Labiatae	*Salvia moorcroftiana* Wallich	Butkhela, Ghalighi (Swat) & Mayyar (Dir)
Solanaceae	*Datura* sp.	Dir
	Lycopersicon esculentum Miller	Bahawalpur & Peshawar
	Nicotiana tabacum L.	Peshawar, Swat, Bahawalpur, Sahiwal & Haripur
	Solanum tuberosum L.	Peshawar, Swat, Lahore & Haripur
Scrophular-iaceae	*Veronica* sp.	Dir
Compositae	*Achillea millefolium* L.	Dir
	Artemisia sp.	Talash (Dir)
	Calendula arvensis L.	Timurgarha
	Carduus nutans Hooker f.	Kaghan
	Carthamus lanatus L.	Dir
	C. oxyacantha Bieberstein	Rawalpindi
	Xanthium strumarium L.	Rawalpindi

NATURAL ENEMIES IN PAKISTAN

Mohyuddin (1981) and CIBC (1982) have reported eight species of parasites from *H. armigera* (Table 2). These are discussed below.

Table 2. Parasites recorded from Heliothis armigera in Pakistan

Family and species	Host plant	Maximum incidence recorded %	Distribution and altitude (m)
Hymenoptera			
Ichneumonidae			
Campoletis chlorideae Uchida	Tobacco, sugarbeet, maize, tomato, okra, chickpea, wheat, potato	39.6	Peshawar, Sahiwal, Bahawalpur, Murree, Hyderabad, Rawalpindi (20–2170 m)
? *Enicospilus* sp.	Potato	4.8	Lahore (215 m)
Netelia (*Netelia*) *ocellaris* (Thomson)	Chickpea	2.0	Rawalpindi (510 m)
Braconidae			
Apanteles sp.	Tobacco, tomato, okra	6.7	Peshawar, Haripur (360–600 m)
Bracon hebetor Say	Chickpea	2.0	Faisalabad (180 m)
Trichogrammatidae			
Trichogramma chilonis Ishii	Potato	23.0	Lahore, Rawalpindi (215–510 m)
Diptera			
Tachinidae			
Exorista xanthaspis Wiedemann	Clover	4.0	Haripur (600 m)
Palexorista sp.	Potato	0.8	Sahiwal (170 m)

Hymenoptera

Ichneumonidae

1. *Campoletis chlorideae* Uchida: This solitary larval endoparasite was described by Uchida (1957) from adults reared from *Phthorimaea operculella* (Zeller) and *H. assulta* in Japan. It occurs in southwest Asia, China, and the Far East.

In Pakistan it is a widely distributed parasite of noctuid pests and is most important on *H. armigera*. At Murree, it parasitized 19.2% larvae of this pest on wheat in April; at Haripur, 22.2% on potato in April; at Peshawar, 27% and 5.2% on tobacco in May and July, respectively, and 16.6% on sugarbeet in May; at Rawalpindi, 11% on chickpea in May; at

Sahiwal, 25% on tobacco and 39.6% on potato in April and 4.2% on potato in December; at Bahawalpur, 7.6% on tomato, 3.3% on tobacco, and 1.6% on okra in April; and at Hyderabad 12.5% on maize in April (CIBC 1981; 1982).

C. chlorideae has been recorded not only on *H. armigera* but also on other noctuids. It parasitized 6.7% larvae of *Mythimna* spp. on maize in June and 1.3% in July at Murree; 6.1% larvae of *Agrotis* spp. on potato in April; 0.6% *Spodoptera litura* (F.) on cauliflower in September and 1.3% in October at Haripur; 2% larvae of *Mythimna separata* (Walker) in April and 1.5% in June on sugarcane at Peshawar; 1.4% of *Agrotis* spp. larvae on potato in April, 5.7% *Spodoptera exigua* (Hübner) and 25% *S. litura* on maize in September, and 2.2% *S. litura* on cauliflower in October at Rawalpindi; 1.6% of *S. litura* on bitter gourd at Bahawalpur and 0.7% of *S. litura* on spinach in December at Hyderabad (CIBC 1981; 1982).

This parasite was introduced from Pakistan into Western Australia and has been recovered in small numbers repeatedly (Michael et al. 1984). It was also introduced into Trinidad (Yaseen 1979) but establishment has not been documented. The biology of this parasite has been studied in India by Basarkar and Nikam (1982) and Nikam and Basarkar (1978).

2. *Enicospilus* sp.: This is a solitary endoparasite, and it was reared from *H. armigera* on potato (parasitism 4.8%) in December at Lahore (CIBC 1981).

3. *Netelia ocellaria* (Thomson): This is a solitary larval endoparasite, and it was reared from 2% larvae of *H. armigera* on chickpea in May at Rawalpindi (CIBC 1982).

Braconidae
4. *Apanteles* sp.: This is a solitary larval endoparasite, and it was reared from 1.1% larvae of *H. armigera* on tobacco in May; 4.3% larvae on tomato in June, and 6.7% on okra in June at Peshawar; and 1.7% larvae on tobacco in June at Haripur (CIBC 1982).

5. *Bracon hebetor* Say (*Habrobracon ? hebetor*): This is a solitary larval endoparasite, and it was reared from 2% of *H. armigera* larvae collected from chickpea in April at Faisalabad (CIBC 1982).

Trichogrammatidae
6. *Trichogramma chilonis* Ishii: This is a gregarious egg parasite. According to Nagarkatti and Nagaraja (1979), *Trichogramma australicum* Girault and *T. confusum* Viggiani are synonyms of *T. chilonis*. This parasite has been reported from a large number of species from India, Taiwan, Philippines, Sri Lanka, Japan, Pupua-New Guinea (Nagarkatti and Nagaraja 1971); Malaysia and southwestern Australia (Nagarkatti and Nagaraja 1979); and China, Hawaii, and Guam (Oatman et al. 1982).

In Pakistan it was recorded from *Chilo infuscatellus* Snellen, *C. partellus* (Swinhoe), and *H. armigera* (Mohyuddin 1981); *Bactra* spp. (Habib 1976) *Agrotis ipsilon* L., *Autographa nigrisigna* (Walker), and *Spodoptera litura*.

T. chilonis is apparently a natural parasite of *Heliothis* spp. It has been reported from *H. armigera* in China (Li 1982); India (Yadav and Patel 1981); and Thailand (Supharngkasen 1979). Additionally, it has been reported on *H. assulta* in Japan (Nagarkatti and Nagaraja 1971) and from *H. zea* (Boddie) in Hawaii (Oatman et al. 1982).

Diptera

Tachinidae

7. *Exorista xanthaspis* Wiedemann: This is a solitary larval endoparasite. It has been reared from *H. armigera* larvae (4% of the larvae collected) on clover (*Trifolium alexandrinum*) in April at Haripur (CIBC 1982).

8. *Palexorista* sp.: This solitary larval endoparasite was reared from 0.8% of the *H. armigera* larvae collected from potato plants in November at Sahiwal (CIBC 1981).

DISCUSSION AND CONCLUSIONS

In the past, *H. armigera* and *H. assulta* have been probably often been classified as the same species; consequently, parasites reared in Pakistan have been assigned to *H. armigera*. Obviously, these two species need to be separated in the future, and detailed studies may reveal the presence of additional *Heliothis* species.

General surveys in Pakistan have revealed eight species of parasites attacking *H. armigera*; however, no similar surveys have been conducted on predators and pathogens. So, further surveys will probably yield more parasites and numerous predators and pathogens.

Of the parasites reported from Pakistan, *Campoletis chlorideae* seems suitable for trial in several countries, especially where this genus is not present on *Heliothis* spp. It occurs over a wide range of climatic conditions, varying from temperate to tropical. It attacks a number of noctuid pests but prefers *H. armigera* as a host. Thus, it may survive on other pest species when *Heliothis* spp. are either absent or rare.

T. chilonis and *Cotesia* (=*Apanteles*) sp. have been so far recorded only from areas having a tropical climate with summer rains. Further surveys may detect them in other areas as well. *T. chilonis* can be recommended for release trials in Europe and the USA.

No evaluations have been conducted on predators in Pakistan. Although a number of these have been listed from various parts of the

world by Greathead and Girling (1982) and King et al. (1982), their introduction has not been considered because they are general feeders. Greathead and Girling (1982) surmised that prospects for establishing predators are poor; in fact, predators may be detrimental if they start feeding on beneficial insects.

Of the numbers of parasites reported worldwide, only a few can be considered for introduction, because most of them are incidental. This considerably reduces the number of species available for introduction; for example, of the 37 species reported by Achan et al. (1968) from India, only 8 are important. Furthermore, if the species already present in Pakistan as major parasites and species with incomplete identification are deleted, only three species remain to be tried as introductions. Similarly, the number of species that can be considered for introduction from India, Uganda, Europe, and the USA is drastically reduced.

H. armigera has a number of generations in Pakistan, therefore, parasites attacking multivoltine species should have priority. For example, *Banchopsis ruficornis* (Cameron), though an important parasite, has only one generation a year (Achan et al. 1968); thus, it may be effective only in areas where *H. armigera* has one or two generations.

All the parasites recorded in Pakistan, except *Trichogramma chilonis,* are larval parasites. Therefore, the larval-pupal tachinid *Archytas marmoratus* (Townsend) from the USA and *Goniophthalmus halli* Mesnil from India should receive high priority for introduction. Theoretically, these parasites will fill empty niches and competition with indigenous parasites will be minimized.

Again, to begin with, species belonging to the genera that are already present have been omitted; for example, although *Campoletis sonorensis* (Cameron) is an important parasite in the USA, it has not been included in the list because a closely related species, *C. chlorideae,* is an important parasite in Pakistan. Moreover, as reported by King et al. (1982), *C. chlorideae* proved superior in competition with *C. sonorensis* in the USA.

Parasites and predators of related species and genera have provided successful biological control in many cases (Pimentel 1963; Carl 1982); so, parasites of *H. zea* and *H. virescens* have also been included in the list of parasites for trial in Pakistan.

Parasites suggested for evaluation in Pakistan, using the above criteria, are listed in Table 3. These were selected from the numerous species reported from *H. armigera* by Parsons (1940) from South Africa, Coaker (1959) from Uganda, Reed (1965) from Tanzania, and Achan et al. (1968) from India. Parasites from *H. zea* and *H. virescens* (F.) have been reported from the USA by Ridgway and Lingren (1972), Snow et al. (1966), and Lewis and Brazzel (1968). Room (1979) and Bishop and Blood (1977) have reported natural enemies from Australia but not their degree of incidence.

Table 3. Parasites recorded from Heliothis *spp. suggested for evaluation in Pakistan*

Family and species	Distribution	Reference
Hymenoptera		
Ichneumonidae		
Banchopsis		
ruficornis (Cameron)	India	Achan et al. (1968)
Enicospilus sp. ?		
communis Szepligeti	Uganda	Coaker (1959)
Heteropelma		
scaposum (Morley)	Australia	King et al. (1982)
Hyposoter didymator	Israel,	Bar et al. (1979),
(Thunberg)	Europe	Carl (1978)
Braconidae		
Apanteles kazak		
Telenga	USSR, Europe	Rustamova (1981)
		Carl (1978)
Bracon brevicornis	Egypt, India,	King et al. (1982)
Wesmael	South Africa,	Achan et al. (1968)
	USSR	Bogush (1957)
Cardiochiles nigricollis (Cameron)	South Africa	CIBC (1978)
C. nigriceps Vierick	USA	King et al. (1982)
C. trimaculatus (Cameron)	Uganda	Coaker (1959)
Microplitis croceipes (Cresson)	USA	Snow et al. (1966)
		Lewis & Brazzel (1968)
M. demolitor Wilkinson	Australia	King et al. (1982)
Scelionidae		
Telenomus sp. nr. *triptus* Nixon	Australia	Twine (1973)
Diptera		
Tachinidae		
Archytas marmoratus (Townsend)	USA	Shepard and
		Sterling (1972)
Carcelia illota Curran	India	Achan et al. (1968)
Eucelatoria bryani Sabrosky	USA	King et al. (1982)
Goniophthalmus halli	India,	Achan et al. (1968),
Mesnil	South Africa,	King et al. (1982)
	Tanzania	Reed (1965)

Thus the most important parasites could not be selected from these publications. However, King et al. (1982) and Twine (1973) reported important parasites from Australia and seemingly promising parasites from Australia for introduction in Pakistan are also listed (Table 3).

The parasites that have been omitted at this stage could be considered later, because different strains of the same species or minor parasites in the native home may prove more efficacious in a new ecosystem. For example, Mohyuddin and Shah (1977) and Cumber et al. (1977) reported that although *Apanteles ruficrus* Haliday was present in New Zealand, the

Pakistan strain when introduced in 1974 gave excellent control of *Mythimna separata.*

In Pakistan, *H. armigera* has been reported from 40 plant species that were recorded in a survey carried out for various pests and their natural enemies. No study has been made on its population trends on various host plants and their effect on population buildup on major crops. The importance of such studies cannot be ignored if control measures are to be developed.

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Distribution and Economic Importance of *Heliothis virescens* and *Heliothis zea* in North, Central, and South America and of Their Natural Enemies and Host Plants

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ABSTRACT

Heliothis virescens and *Heliothis zea* are two of the most important insect pests of the principal field (corn, cotton, soybeans, and tobacco) and horticultural (garden beans, sweetcorn, and tomato) crops on the American continent. As of September 1985, we have had access to a database containing 7717 documents on *H. zea* and *H. virescens* (the Soybean Insect Research Information Center, or SIRIC, of the University of Illinois at Urbana-Champaign). A compilation of host plants, parasitoids, and predators of *H. zea* and *H. virescens* is presented, based on the holdings of this database. The two species have been recorded from 235 plant species in 36 families. The parasitoids are equally divided among the Hymenoptera (60 species in 6 families) and Diptera (61 species in 4 families), and the predators are representative of 8 Insecta and 2 Arachnida orders, including a total of 142 species. We conclude from the examination of this literature that there is a dire need for a more coordinated effort to survey the natural enemies of *Heliothis* spp., keeping careful records of host-plant association and growth stage of pest attacked (age-specific predation or parasitism).

INTRODUCTION

Since 1969, the soybean entomology project of the University of Illinois and the Illinois Natural History Survey has searched, collected, and stored the literature on arthropods associated with soybean (Kogan and Luckmann 1971; Kogan and Kogan 1984). In 1971, storage and retrieval operations were computerized and the database became known as the Soybean Insect Research Information Center (SIRIC). Documents included in the

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database consist of those dealing with herbivores on soybeans and the methods to control them on that crop (this is the SoyEnt collection). The SoyEnt collection contains about 5000 documents, and a comprehensive worldwide bibliography of soybean entomology is being prepared for publication (Kogan et al. in preparation). In addition, exhaustive searches have been done on species of key importance to soybean, independent of the crop association. *Heliothis virescens* and *Heliothis zea* are two such species (Kogan et al. 1978). The sum total of the SoyEnt plus the literature on major species constitutes the SIRIC collection which contains about 23,000 documents. The *"Heliothis"* database for the American continent alone contains 7717 documents; these represent 33% of the total SIRIC collection, demonstrating the vigor of *Heliothis* research in the region.

This paper has been developed on the holdings of the SIRIC database. We first demonstrate, using the soybean literature, that there is a close correlation between economic importance of a pest and the literature output on the pest. We then extrapolate this criterion to estimate the relative importance of the *Heliothis* complex on the major crops, and the relative importance of its common natural enemies. We extracted from a representative sample of the literature the host plants, geographic range, parasitoids, and predators of *Heliothis* spp. in the American continent. Checklists of host plants, parasitoids, and predators are appended.

ECONOMIC IMPORTANCE OF PESTS AND LITERATURE OUTPUT

Entomologists tend to concentrate their efforts on what they perceive are the most important pest problems, although assessment of importance is often subjective. This intuitive perception of relevance, however, has not been explicitly demonstrated. The SoyEnt file should help us demonstrate that species with the greatest economic impact tend to receive the largest proportion of research effort, expressed in terms of numbers of papers published. Two sets of data were used in this analysis. One for North America was based on Kogan (1979), and a second, for Japan, was based on Kobayashi (1977).

The North American data set ranked the most important species of soybean insect pests by state, based on the frequency of insecticide use over 10-year periods and the area in the state treated for the control of each pest. A pest impact index was computed by multiplying the frequency of occurrence (0-100% in decimal form) by the percent of the crop area treated with insecticides (also in decimal form). The resulting value was then multiplied by a weight factor to correct for differences in total area planted to the crop in the various states; this constitutes the relative pest impact index. Table I lists the indexes for the eight soybean pests that account for more than 85%

Table 1. Correlation between number of papers in database and economic importance of pests in the USA, based on: SoyEnt File n = 4777 documents and SIRIC File n = 22,824 documents

Species	Index of pest impact[1]	Number of papers	
		SoyEnt	SIRIC
Heliothis zea + H. virescens	4.47	803	7715
Anticarsia gemmatalis	3.49	796	1053
Nezara viridula	3.35	681	1359
Plathypena scabra	3.01	513	684
Pseudoplusia includens	2.69	461	590
Epilachna varivestis	1.90	553	1698
Cerotoma trifurcata	1.23	464	735
Acrosternum hilare	0.72	168	289

[1] Based on Kogan (1979).

of the total amount of insecticides applied to the crop in the USA. The number of papers in the SoyEnt and SIRIC files are also listed. Figure 1 shows the very good correlation that exists between pest impact index and number of papers in the SoyEnt, the more restricted, and, in this case, the more representative, of the two files. A similar analysis was conducted using the data from Japan (Kobayashi 1977), but here pest impact was a subjective assessment of the author on a scale of 1 (low impact) to 3 (great
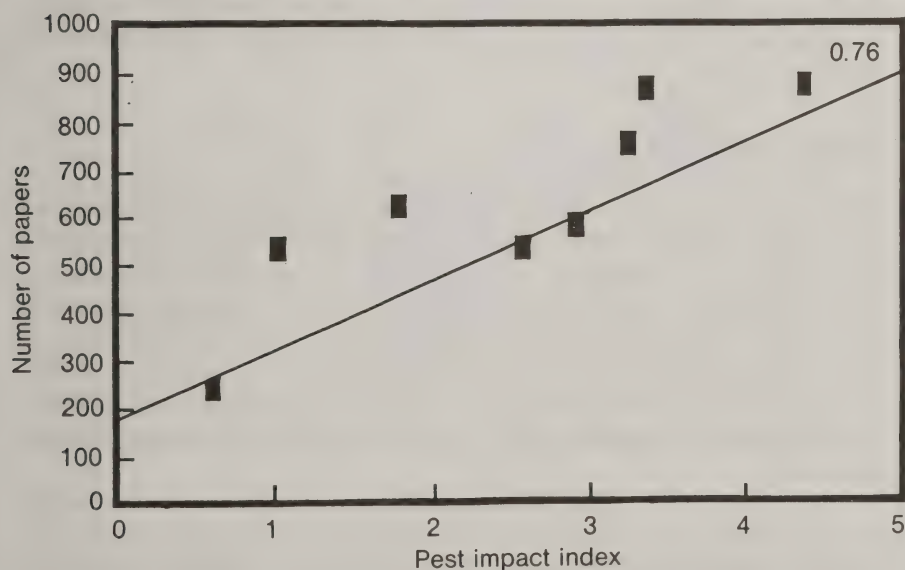
Figure 1. Correlation between pest impact index and number of papers in the SoyEnt file (based on Kogan 1979).

Table 2. Correlation between number of papers in database and economic importance of pests in Japan, based on: SoyEnt File n = 4777 documents and SIRIC File n = 22,824 documents

Species	Index of pest impact[1]	Number of papers	
		SoyEnt	SIRIC
Nezara viridula + N. antennata	3.00	720	1,401
Etiella zinckenella	3.00	226	297
Leguminivora glycinivorella	3.00	169	173
Aphis glycines	2.00	113	115
Dolycoris baccarum	2.00	35	35
Syllepta ruralis	2.00	35	35
Melanagromyza sojae	1.00	102	103
Anomala rufocuprea	1.00	62	63
Paraluperodes nigrobilineatus	1.00	38	38

[1]Based on Kobayashi (1977).

impact) (Table 2). The correlation is far less perfect, particularly due to *Melanagromyza sojae,* a common pest of questionable economic importance that has received more attention from Asian researchers than it probably deserves (except, perhaps, when infestations occur very early in the season).

In summary, there seems to be good agreement between what is perceived as an important pest problem and the effort invested in its research. With this understanding, we will try to do a similar bibliometric analysis on geographic range, host crops, and natural enemies of *Heliothis virescens* and *H. zea.*

GEOGRAPHIC RANGE

No attempt was made to update the geographic range maps published by the USDA and reproduced in our *Heliothis* bibliography (Kogan et al. 1978) (Figure 2). According to those maps, *H. zea* is the more widely dispersed species, occurring over the entire North American continent (except northern Canada and Alaska), the whole of Central America and the Caribbean Islands, and South America (with the exception of the Chilean and Argentinean Patagonia, the Brazilian Amazon, and parts of the northeastern Brazilian states). In addition, *H. zea* is recorded from Hawaii.

The range of *H. virescens* is considerably more disjunct. In South America, there are no apparent records from the Guianas, Ecuador, Paraguay, and much of Argentina, Chile, and northern Brazil. It is uncertain whether this record results from truly disjunct dispersion, from incomplete surveys, or from misidentifications. Table 3 shows the concen-

Figure 2. Distribution of *Heliothis zea* and *H. virescens* on the American continent (Redrawn by permission from Commonwealth Institute of Entomology, 1967).

Table 3. Counts of number of papers from New World countries on Heliothis *spp.,* H. zea, *and* H. virescens

Country	*Heliothis* spp.	*H. zea*	*H. virescens*
Antigua	7	6	1
Argentina	37	30	12
Bahamas	4	4	—
Barbados	12	10	7
Belize	2	2	1
Bermuda	5	5	—
Bolivia	4	4	1
Brazil	118	103	47
Canada	161	156	15
Chile	22	21	4
Colombia	29	24	21
Costa Rica	2	2	—
Cuba	25	10	20
Dominican Republic	1	1	—
Ecuador	—	—	—
El Salvador	13	12	2
French Antilles	—	—	- -
French Guiana	—	—	—
Grenada	1	—	1
Guadeloupe	4	3	2
Guatemala	6	6	2
Guyana	—	—	—
Haiti	3	3	—
Honduras	4	4	1
Jamaica	21	20	3
Martinique	—	—	—
Mexico	201	172	112
Netherlands Antilles	—	—	—
Nicaragua	13	12	4
Panama	5		
Paraguay	—	—	—
Peru	77	30	67
St. Vincent	2	2	—
Surinam	4	4	—
Trinidad	5	3	3
Uruguay	5	5	2
USA			
Continental USA	6,469	5,691	2,119
Alaska	—	—	
Hawaii	91	87	6
Puerto Rico	44	33	17
Virgin Islands	41	26	27
Venezuela	22	15	13

tration of effort in *Heliothis* research in the American continent. The overwhelming dominance of the North American literature (USA and Mexico), directly reflects differences in numbers of scientists and age of the research establishments in North and South America, but it also indirectly reflects the relative importance of the pest in the two regions. If corrected for the size of the research establishment in the two regions (a ratio of about 12 to 1, to judge from memberships in the professional societies) the output per scientist would still be about 6 to 1 in North America. Since the *Heliothis* species are present in both regions and on similar crops, it is necessary to investigate why *Heliothis,* in general, is a lesser problem in the south than in the north of the continent. Exhaustive surveys of natural enemies are wanting in South America, with the exception of Colombia (Hallman 1980).

HOST-PLANT RANGE

Both *H. zea* and *H. virescens* are general feeders and frequently become major pests of field, vegetable, fruit, ornamental, and forage crops. Additionally, they choose many wild, uncultivated hosts, which may be of major importance during periods when crops are not available, either in early spring or again in late fall prior to overwintering. The most extensive listings of hosts for *H. zea* and *H. virescens* have appeared only recently. Stadelbacher et al. (1986) surveyed the wild hosts of *Heliothis* spp . in the southern USA, listing 89 species in over 14 plant families; Hallman (1980) surveyed *Heliothis* hosts in Colombia (South America) and listed 74 species in 20 families, including 8 important agricultural crops. The total number of cultivated and wild hosts recorded in Table 4 includes 238 species in 36 families. Nearly one-third of these are in the family Leguminosae, while an additional third is comprised of species in the families Solanaceae, Malvaceae, and Compositae. Based on the research effort devoted to these pests, it is apparent that *Heliothis* spp. are major pests of corn, cotton, soybean, tomato, and tobacco (Table 5). Since number of researchers devoted to a given crop is often correlated to the area planted to the crop and the crop's relative economic value, it is apparent that *Heliothis* must be more intensely studied in tomato (ratio of number of papers to area planted = 0.00159/ha) than in corn (ratio = 0.0000364), by a factor of 43.6 in favor of tomato, suggesting that fewer tomato researchers devote more individual effort to this pest than corn researchers do.

This checklist does not include every plant species from which *H. zea* or *H. virescens* eggs were recovered, nor does it include species regarded as very poor hosts by a specific author. More detailed accounts of seasonal availability, suitability, and relative abundance of many plants in this

Table 4. *Checklist of cultivated and wild hosts of Heliothis virescens (V) and H. zea (Z) in North, Central, and South America*

Family Host plant	Species of Heliothis	Geographic range	Reference[a]
Acanthaceae			
Ruellia lorentziana Grisebach	V, Z	Colombia	10
Ruellia runyoni Tharp & Barkl	V, Z	TX[b]	22
Amaranthaceae			
Amaranthus spp.	Z	NC	13
		USA	14
Amaranthus palmeri (Watts)	Z	TX	22
Asclepiadaceae			
Sarcostema clausa (Jacq.)	V	Colombia	10
Boraginaceae			
Cordia globosa (Jacq.) HBK	V	Colombia	10
Heliotropium indicum L.	V	Colombia	9
Cannabinaceae			
Cannabis sativa L.	Z	USA	14
Cannaceae			
Canna indica L.	Z	USA	14
Capparadaceae			
Cleome spinosa Jacq.	V	Colombia	9
	V, Z	MS	16, 22
	V	Virgin Islands	19
Pedicellaria pentaphylla (L.) Schrank = *Cleome gynandra* L.	Z	GA	2, 22
Chenopodiaceae			
Chenopodium spp.	Z	USA	14
Compositae			
Acanthosperum hispidum DC.	V	Colombia	9
Ageratum spp.	V	Peru	11

Calendula officinalis L.	V	Peru	11
Chrysanthemum sp. L.	V	Colombia	9
	N	LA	6
Cichorium intybus L.	V	Uruguay	4
Cynara scolymus L.	N	Uruguay	4, 5
Erigeron canadensis L.	V	USA	14
Haplopappus divaricatus (Nutt.) A. Gray	V, Z	GA	2, 22
	V	MS	16, 22
Helianthus annuus L.	N	Brazil	3
	Z	Uruguay	4, 5
	V, Z	Cuba	7
	V	Colombia	9
	N	USA	14
Helianthus debilis Nutt.	N	Uruguay	4, 5
Helichrysum bracteatum (Ventem.) Andr.	V	Peru	11
Heterotheca subaxillaris (Lam.) Britton & Rusby	V	GA	2, 22
Lagascea mollis Cavanilles	V	Colombia	9
Pseudoelephantopus spicatus (BJ&A) C.F. Baker	V	Colombia	9
Stilias caroliniana (Walt.) Raf. =			
Pyrrhopappus carolinianus (Walt) DC	V	GA	2, 22
Tagetes spp.	N	Chile	1
Tridax procumbens L.	V	Colombia	9
Trixis radialis (L.) Kuntze	V	Colombia	9
Veronia brachiata Benth.	V	Colombia	9
Veronia brasiliana (L.) Druce	V	Colombia	9
Xanthium sp.	N	GA	2, 22
	N	USA	14
Xanthium pennsylvanicum Wallr.	V, Z	MS	16

Table 4 continued

Family / Host plant	Species of Heliothis	Geographic range	Reference[a]
Convolvulaceae			
Ipomoea spp.	V	GA	2, 22
	V, Z	SC	22
Ipomoea commutata R&S	V	Colombia	9
Ipomoea nil (L.) Roth	Z	USA	14
Ipomoea purpurea (L.) Roth	V	Colombia	10
Ipomoea trichocarpa (Ell.)	V	NC	13
Ipomoea triloba L.	V	TX	22
Jaquemontia sp.	V	Colombia	9, 10
Jaquemontia tamnifolia (L.) Raf.	V	Colombia	9
	V, Z	LA	6, 22
Merremia cissoides (Lam.) Grisebach	V, Z	Colombia	10
Merremia umbellata (L.) Hall	V	Colombia	10
	V	Colombia	10
Cruciferae			
Brassica oleracea L. var. acephala	V, Z	FL	12
	Z	USA	14
Brassica oleracea L. var. capitata	Z	Chile	1
	V, Z	FL	12
	Z	USA	14
Cucurbitaceae			
Citrullus vulgaris Schrad	Z	Uruguay	4, 5
	V	Colombia	9
Cucumis melo L.	Z	USA	14
	V	Colombia	9
Cucumis sativus L.	Z	USA	14
	Z	Uruguay	4, 5
	Z	USA	14

Taxon		Location	Reference
Cucurbita sp.	Z	Cuba	7
Cucurbita maxima Duchesne	V	Colombia	9
Cucurbita pepo L.	Z	Uruguay	4, 5
	V	Peru	11
	Z	USA	14
Sicyos angulatus L.	V	MS	22
Euphorbiaceae			
Acalypha spp.	V, Z	MS	22
Acalypha alopecuroides Jacq.	V	Colombia	10
Acalypha infesta Poepp.	V	Peru	11
Caperonia palustris (L.) St. Hil.	V	Colombia	9, 10
Croton hirtus L. Her	V, Z	Colombia	9, 10
Ricinus communis L.	V	Colombia	10
Geraniaceae			
Geranium sp.	V	Colombia	9
	V	Peru	11
	Z	USA	14
Geranium carolinianum L.	V, Z	MS	18, 20, 21, 22
	V, Z	GA	18, 22
	V, Z	SC	18, 22
Geranium dissectum L.	V, Z	MS	20, 21, 22
Pelargonium sp.	V	Colombia	9
Gramineae			
Chaetocloa italica = *Setaria italica* (L.) Beauv.	V, Z	FL	12
Panicum sanguinale L.	Z	USA	14
Panicum scoparium Lam.	Z	USA	14
	Z	GA	2, 22

Table 4 continued

Family Host plant	Species of Heliothis	Geographic range	Reference[a]
Panicum texanum Buckl.	Z	TX	14
Saccharum officinarum L.	Z	Southern USA	14
Sorghum halepense (L.) Pers.	Z	MS	16
Sorghum vulgare (L.) Pers.	Z	GA	2
	Z	LA, AR	6
	Z	Colombia	9, 10
	Z	FL	12
	Z	USA	14
Triticum aestivum L.	Z	MS	16
Zea mays L.	Z	Chile	1
	Z	Chile	1
	Z	GA	2
	Z	Brazil	3, 14
	Z	Uruguay	4, 5
	Z	LA, AR	6
	Z	Cuba	7
	Z	Colombia	9, 10
	Z	FL	12
	Z	USA	14
	Z	Puerto Rico	14
	Z	MS	16, 20
Iridaceae			
Gladiolus sp.	Z	USA	14
Labiatae			
Hyptis aff. *mutabilis* (A. Rich) Briq.	V	Colombia	10
Hyptis suaveolens (L.) Poit	V	Colombia	10
Leonotis nepetaefolia (L.) R. Brown	V	Colombia	9, 10
Salvia occidentalis Sw.	V	Colombia	10

Salvia officinalis L.	V	Peru	11
Salvia riparia Kunth	V	Colombia	9
Stachys agraria Cham. & Schlecht	Z	TX	14
Leguminosae			
Aeschynomene americana L.	V	Colombia	9, 10
Aeschynomene brasiliana (Poir.) DC	V	Colombia	10
Aeschynomene ciliata Vogel	V	Colombia	10
Aeschynomene rudis Benth.	V	Colombia	10
Arachis hypogaea L.	Z	Uruguay	4
	V, Z	Colombia	9, 10
	V, Z	FL	12
	Z	MS	16
Astragalus caryocarpus Ker	Z	USA	14
Cajanus cajan (L.)	V	Cuba	7
	V	Peru	11
	V	Virgin Islands	19
Cajanus indicus (L.)	V	Colombia	9
Cassia occidentalis L.	V	Colombia	10
Cassia patellaria (DC.) Greene	V	Colombia	10
Cassia reticulata (Willd.) Pittier	V	Colombia	10
Cassia rotundifolia (Pers.) Greene	V	Colombia	10
Cassia tora (L.) Br. & Rose	V	Colombia	9, 10
Cicer arietinum L.	V	Cuba	7
	V	Peru	11
Crotalaria spp.	Z	GA	2
	Z	LA	6
	V	Colombia	9
	Z	MS	16

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Table 4 continued

Family Host plant	Species of Heliothis	Geographic range	Reference[a]
Crotalaria pallida Aiton	V	Colombia	10
Crotalaria retusa L.	V	Colombia	10
Dalea pogonathera Gray	V	TX	22
Desmodium spp.	V, Z	NC	13
	V	Virgin Islands	19
	V, Z	FL	22
	V	GA	22
	V	SC	22
Desmodium canum (Gemel) Schinz & Thell.	V	Colombia	9
Desmodium purpureum (Mill.) Fawc & Rendle	V, Z	GA	17
Desmodium rigidum (Ell.) DC	V, Z	MS	16, 22
Desmodium scorpiorus (Sw.) Desv.	V	Colombia	10
Desmodium tortuosum (Sw.) DC. = *Meibomia purpurea* (Mill.) Vail	V	Colombia	10
	V, Z	GA	2, 22
Dolichos lablab L.	V	Peru	11
	V	SC	22
Erythrina herbacea L.	Z	USA	14
Galactia striata (Jacq.) Urban	V	Colombia	10
Glycine max (L.) Merrill	Z	GA	2
	Z	Uruguay	4
	V, Z	LA, AR	6
	V, Z	Colombia	9, 10
	V, Z	FL	12
	Z	MS	16, 20
Indigofera anil L.	V	Colombia	9
Indigofera hirsuta L.	V	Colombia	10

Lathyrus hirsutus L.	V, Z	MS	20, 21, 22
Lathyrus latifolius L.	Z	MS	16
Lathyrus odoratus L.	V	Uruguay	4
	V	Peru	11
Lens culinaris Medik.	V	Uruguay	4
Lespedeza spp.	N	GA	22
Lespedeza bicolor Turcz.	V	SC	22
Lespedeza sericea (Thumb.) Benth.	N	GA	2
	V, Z	MS	16
Lespedeza stipulacea Maxim	Z	AR	6
Lupinus spp.	Z	AR	22
Lupinus var. Hastings White	V, Z	LA	6, 22
Lupinus texensis Hooker	V, Z	TX	8, 22
Medicago hispida Gaetn.	V, Z	LA	6
	N	MS	16
	N	AR	22
Medicago lupulina L.	V, Z	MS	16, 20
Medicago polymorpha L.	N	MS	20
Medicago sativa L.	N	Chile	1
	N	Uruguay	4
	V, Z	LA, AR	6, 22
	V, Z	MS	16, 20, 21, 22
	N	USA	14
	V, Z	TX	22
	N	SC	22
Meibomia canescens (L.) Kuntze	V	GA	2
Meibomia stricta (Pursh) Kuntze	V	GA	2
Melilotus alba Desr.	V	MS	16
Melilotus albus Lam.	N	TX	22
	N	AR	22

(continued)

Table 4 continued

Family Host plant	Species of *Heliothis*	Geographic range	Reference[a]
Melilotus officinalis Lam.	Z	AR	22
Mimosa comporum Benth.	V	Colombia	10
Mimosa invisa Mar.	V	Colombia	10
Mimosa pigra L.	V	Colombia	10
Mimosa somnians H & B	V	Colombia	10
Phaseolus limenses Macfad.	Z	LA, AR	6
Phaseolus vulgaris L.	V, Z	Chile	1
	Z	GA	2
	V	Uruguay	4
	Z	AR	6
	V	Colombia	9
	V	Peru	11
	Z	USA	14
	Z	MS	16
Pisum sativum L.	Z	Brazil	3
	V, Z	Uruguay	4, 5
	Z	USA	14
Pisum sativum L. var. *arvense* (L.) Poir	Z	FL	12
Rhyncosia apoloensis (Rusby) Macbride	V	Colombia	10
Rhyncosia minima (L.) DC.	V	Colombia	9, 10
Stizolobium deeringianum (Bort.) Merrill	V	Colombia	9
Stylosanthes gracilis HBK	V	Colombia	9
Trifolium campestre Schreb	Z	MS	20
Trifolium hybridum L.	Z	AR	22

Species		Location	
Trifolium incarnatum L.	V, Z	LA	6, 22
	V, Z	MS	16, 20, 21, 22
	V	TX	22
	Z	SC	22
	Z	AR	22
Trifolium pratense L.	V, Z	LA	6
	Z	MS	20
	Z	AR	22
Trifolium procumbens L.	Z	MS	16
	Z	AR	22
Trifolium repens L.	Z	AR	22
	V, Z	LA	6, 22
	V, Z	FL	12
	Z	MS	16
Trifolium resupinatum L.	V, Z	MS	16, 21, 22
	Z	AR	22
	Z	TX	22
	Z	GA	22
Vicia spp.	Z	AR	22
Vicia sativa L.	Z	GA	2
Vicia villosa Roth	V, Z	LA	6, 22
	V, Z	MS	20, 21, 22
	Z	SC	22
Vigna sinensis (L.) Endl.	Z	LA	6
	Z	Cuba	7
	V	Colombia	9
	Z	USA	14

(continued)

Table 4 continued

Family Host plant	Species of *Heliothis*	Geographic range	Reference[a]
Liliaceae			
Allium cepa L.	Z	Chile	1
Linaceae *Asparagus officinalis* L.	Z	Uruguay	4
	Z	USA	14
Linum usitatissimum L.	Z	Chile	1
	V, Z	GA	2
	Z	Brazil	3
	V, Z	Uruguay	4, 5
	V	Peru	11
Malvaceae			
Abelmoschus moscatus M.	V	Colombia	9
Abutilon theophrasti Medik	V, Z	AR	6
	V, Z	MS	21, 22
Abutilon trisulcatum Jacq.	V	TX	22
Althaea rosea Cav.	Z	Brazil	3
	V	Uruguay	4, 5
Bastardia viscosa (Kth)	V	Virgin Islands	19
Gossypium hirsutum L.	Z	GA	2
	V, Z	Uruguay	4, 5
	V, Z	LA, AR	6
	V, Z	Cuba	7
	V, Z	Colombia	9, 10
	V, Z	FL	12
	Z	USA	14
	V, Z	MS	16, 20

Species		Location	
Hibiscus esculentus L.	Z	Brazil	2
	V, Z	Uruguay	4
	V	Colombia	9
	Z	USA	14
	V, Z	MS	16
	V	Virgin Islands	19
Hibiscus moscheutos L.	V	MS	16
Hibiscus rosasinensis L.	V	Uruguay	4
	Z	LA	6
Malachra alceifolia Jacq.	V	Colombia	9, 10
Malva borealis Wallm.	Z	USA	14
Malva parviflora L.	V	Uruguay	4
Malvastrum coromandelianum (L.) Garcke	V	Colombia	9, 10
Malvastrum spicatum (L.) Gray	V	Colombia	10
Pavonia sp.	V	Colombia	10
Sida sp.	Z	USA	14
	V	Colombia	9
Sida acuta L.	V	Colombia	10
Sida cordifolia L.	V	Colombia	9, 10
Sida glomerata Cav.	V	Colombia	10
Sida glutinosa Cav.	V	Colombia	10
Sida paniculata L.	V	Colombia	9
Sida procumbens Swartz	V	Colombia	10
Sida rhombifolia L.	V	Colombia	10
	V	NC	13
Sida spinosa L.	V, Z	LA	6, 22
	Z	SC	22
Sida urens L.	V	Colombia	10

(continued)

Table 4 continued

Family Host plant	Species of *Heliothis*	Geographic range	Reference[a]
Melastomataceae			
Rhexia spp.	V	MS	16
Rhexia alifanus Walt.	V	GA	2, 22
	V	NC	13, 22
Rhexia mariana L.	V	SC	22
	V	NC	13, 22
Rhexia nashii Small	V	NC	13, 22
Moraceae			
Ficus carica L.	Z	USA	14
Onagraceae			
Jussiaea decurrens (Walt.) DC	Z	NC	13
Oenothera spp.	Z	AR	22
Passifloraceae			
Passiflora foetida L.	V	Colombia	10
	V	Virgin Islands	19
	V	TX	22
Pedaliaceae			
Sesamum indicum L.	V	Cuba	7
	V	Colombia	9, 10
	V, Z	MS	16
Polygonaceae			
Polygonum pennsylvanicum L.	V, Z	MS	22
Rumex crispus L.	V	GA	2
Portulacaceae			
Portulaca oleracea L.	V	Colombia	9

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Rosaceae			
Fragaria chiloensis (L.) Duchesne	Z	USA	14
Prunus persica (L.) Batsch	Z	USA	14
Pyrus communis L.	Z	CA	14
Rosa spp.	Z	LA	6
	V	Colombia	9
	V	Peru	11
	Z	USA	14
Scrophulariaceae			
Antirrhinum sp.	V	LA	6
Antirrhinum majus L.	V	Peru	11
Castilleta indivisa Englemann	V, Z	TX	8, 22
Linaria canadensis (L.) Dum.	V, Z	GA	2, 22
	V, Z	MS	16
	V, Z	SC	22
Linaria canadensis var. *texana* (Scheele) Ponn.	V, Z	NC	13
Penstemon laevigatus Aiton	V	SC	22
Scoparia dulcis L.	V	Colombia	10
Solanaceae			
Capsicum spp.	Z	Chile	1
	Z	Cuba	7
Capsicum annuum L.	Z	Uruguay	4, 5
	Z	USA	14
Capsicum frutescens L. *grossum*	Z	FL	12
Datura stramonium L.	Z	USA	14
Lycopersicon esculentum Mill.	V, Z	Chile	1
	Z	GA	2
	V, Z	Brazil	3
	V, Z	Uruguay	4, 5
	Z	AR	6
	Z	Cuba	7

Table 4 continued

Family Host plant	Species of *Heliothis*	Geographic range	Reference[a]
	V	Colombia	9
	V	Peru	11
	V, Z	FL	12
	Z	USA	14
	Z	MS	16, 20
Nicandra physaloides (L.) Pers.	V	Peru	11
Nicotiana alata Link & Otto	V	Uruguay	4
Nicotiana paniculata L.	V	Peru	11
Nicotiana repanda Willd.	Z	USA	14
	V, Z	TX	22
Nicotiana rustica L.	V	TX	22
Nicotiana tabacum L.	V, Z	Chile	1
	V, Z	GA	2
	V, Z	Brazil	3
	V, Z	Uruguay	4, 5
	V, Z	LA	6
	V	Cuba	7
	V	Colombia	10
	Z	USA	14
	V	KY	15
	V, Z	MS	16
Petunia spp.	V	Peru	11
Physalis spp.	Z	USA	14
Physalis angulata L.	V	GA	2, 22
	V	Colombia	10
Physalis heterophylla Nees	V	KY	15
Physalis lagascea-glabrescens Schulz	V	Colombia	10

Physalis turbinata Medic.	V	GA	2, 22
Physalis viscosa L.	V	GA	2, 22
Solanum spp.	Z	USA	14
Solanum carolinense (L.) Pers.	V, Z	MS	16
	V	SC	22
Solanum hirtum Vahl.	V	Colombia	10
Solanum melongena L.	Z	Brazil	3
	V	Uruguay	4
	Z	USA	14
	Z	MS	16
Solanum rostratum Dunal	V, Z	MS	16
Solanum sisymbriifolium Lam.	V	GA	2, 22
Solanum torvum Sw.	V	Virgin Islands	16
Solanum tuberosum L.	Z	Chile	1
Sterculiaceae			
Melochia pyramidata (L.) Britton	V	Colombia	9, 10
Waltheria indica L.	V	Colombia	10
Tiliaceae			
Corchurus orinocansis H.B.K.	V	Colombia	9, 10
Turneraceae			
Turnera ulmifolia L.	V	Colombia	10
Verbenaceae			
Petitia sp.	Z	Cuba	7
Priya lappulacea (L.) Persoon	V	Colombia	10
Verbena spp.	V	Peru	11
Verbena neomexicana Gray	V, Z	TX	22

(continued)

Table 4 continued

Family Host plant	Species of *Heliothis*	Geographic range	Reference[a]
Vitaceae			
Vitis sp.	Z	Chile	1
	Z	CA	14

[a]References

1. Angulo & Weigert 1975.
2. Barber 1937.
3. Biezanko et al. 1949.
4. Biezanko et al. 1974.
5. Biezanko et al. 1957.
6. Brazzel et al. 1953.
7. Bruneret et al. 1945.
8. Egeret et al. 1982.
9. Garcia Roa 1976.
10. Hallman 1980.
11. Hambleton 1944.
12. Martin et al. 1976.
13. Neunzig 1963.
14. Quaintance & Brues 1905.
15. Sitchawat & Thurston 1980.
16. Snow & Brazzel 1965.
17. Snow & Burton 1967.
18. Snow et al. 1966.
19. Snow et al. 1974.
20. Stadelbacher 1980.
21. Stadelbacher 1981.
22. Stadelbacher et al. 1986.

[b] Abbreviations of U.S. state names, in the order in which they appear in the table; TX = Texas; NC = North Carolina; MS = Mississippi; GA = Georgia; LA = Louisiana; SC = South Carolina; FL = Florida; AR = Arkansas; CA = California; KY = Kentucky.

Table 5. Number of papers per major crop and area planted to the crop in North, Central, and South America (1980 data)

Crop	Area planted (×10⁶ ha)	Number of papers
Corn	56.1	2042
Soybean	39.1	803
Cotton	9.2	2251
Common bean	8.2	264
Sugarcane	6.6	30
Peanut	1.4	74
Tobacco	0.9	420
Tomato	0.4	638
Alfalfa	?	222

checklist can be found in the articles by Hallman (1980) and Stadelbacher et al. (1985).

PARASITOIDS

A rich complex of parasitoids is normally supported by populations of *H. zea* and *H. virescens* (Table 6). The table lists a total of 121 parasitoids, equally divided between the Hymenoptera (in 6 families) and the Diptera (in 4 families). Two families of Hymenoptera (Braconidae and Ichneumonidae) and one family of Diptera (Tachinidae) contain 18.8% of the parasitoid species on *Heliothis* spp. Five species of *Trichogramma* (Trichogrammatidae) are effective egg parasitoids; *Trichogramma minutum* is the most widely recorded throughout this region. The most common larval parasitoids include *Cardiochiles nigriceps*, *Cotesia marginiventris*, *Microplitis croceipes* (Braconidae), and several species of *Campoletis* and *Hyposoter* (Ichneumonidae). Later instar larvae are most often attacked by tachinids, particularly *Archytas marmoratus*, *Lespesia archippivora*, *L. aletiae*, and five species of *Eucelatoria*, but the braconid *Chelonus insularis* is also an effective parasitoid of larger *H. zea*. In most instances, these more important parasitoids are not specific to either *H. zea* or *H. virescens*, but records for some of the less important species indicate a much greater degree of specificity. Table 7 lists nine of the most common parasitoid species with the corresponding number of papers dealing with them. It is apparent that the research effort concentrates on the species that are deemed to have the major impact on *Heliothis zea* and *H. virescens*, with *Cardiochiles nigriceps* leading the list.

PREDATORS

In preparing the checklist of predators associated with the *Heliothis* complex on the American continent (Table 8), only those species that were

Table 6. Checklist of parasitoids of Heliothis virescens (V) and H. zea (Z) in North, Central, and South America

ORDER Family Parasitoid	Species of *Heliothis* attacked	Host plant of *Heliothis*	Geographic range	Reference[a]
HYMENOPTERA				
Braconidae				
Apanteles militaris (Walsh)	Z	?	N. America, Puerto Rico, Argentina	1
	Z	Corn	CA[b]	2
	Z	?	Eastern USA, CA, TX	28
	Z	Cotton	CA	3
	Z	Soybean	SC	13
	Z	Soybean	NC	38
Apanteles muesbecki Blanch.	sp	Crops	Lesser Antilles, Belize	5
Apanteles theclae Riley	sp	Crops & weeds	TX	17
Bracon hebetor Say	sp	Crops	Lesser Antilles, Belize	5
	Z	Crops	Bolivia	6
Bracon mellitor Say	Z	Soybean	NC	38
Bracon platynotae (Cushman)	Z	Tomato	CA	7
	Z	?	AZ, CA, GA, LA, TX, Mexico	1
Bracon thuberiphagae Mues.	spp	Crops	Lesser Antilles, Belize	5
Cardiochiles nigriceps Viereck	V	?	FL, KS, LA, Mexico	1
	V	Crops & wild hosts	MS	8
	V	Crops & wild hosts	Colombia	9
	V	Cotton, sesame	MS	10
	V	Cotton, tobacco	NC	11
	V	Cotton	AR, TX	12, 15, 18
	V	Crops	SC, AL	13, 14
	V	Weeds	SC	23
	V	Crops & weeds	MS, TX	16, 17

Species				
Chelonus insularis Cresson	V	Tobacco	NC, Cuba	24, 29
	Z	Soybean	NC	38
	Z	Tomato	CA	7
	Z	?	N., C., & S. America, W. Indies, HI	1
	sp	Crops	Lesser Antilles, Belize	5
	Z	Alfalfa, corn	TX	18
	Z	Cotton, alfalfa, corn	AZ	25
Chelonus texanus (Cresson)	Z	Peanut	OK	19
	sp	Alfalfa, corn, cotton, swiss chard	AZ	20
	Z	Cotton	CA	3
	sp	Crops, weeds	TX	17
	Z	Cotton, alfalfa	OK	21
	Z	Corn	CA	2
	Z	?	USA	28
	Z	Cotton	CA	3
	Z	Soybean	NC	38
Cotesia (=*Apanteles*) *marginiventris* (Cresson)	V, Z	Crops & wild hosts	MS	8
	Z	Soybean	SC	22
	V, Z	Cotton, sesame	MS	10
	Z	Peanut	OK	19
	Z	Crops	AL	14
	V, Z	Tobacco, soybean	SC	13
	sp	Weeds	SC	23

(continued)

Table 6 continued

ORDER Family Parasitoid	Species of *Heliothis* attacked	Host plant of *Heliothis*	Geographic range	Reference[a]
	V, Z	?	Eastern and Southwestern, USA, HI, Mexico, W. Indies, northern S. America	1
	Z	Tomato	MS	16
	sp	Cotton	TX, AR	12, 15
	sp	Crops, weeds	TX	17
	Z	?	Bolivia	6
	Z	alfalfa, cotton, potato	TX	18
	Z	?	Eastern USA, TX, W. Indies	28
Meteorus arizonensis Mues.	Z	Soybean	NC	38
Meteorus autographae (Vier.)	Z	Cotton, alfalfa	TX	15, 18
	Z	Soybean	SC	22
	sp	Crops	AL	14
	Z	Soybean	NC	38
Meteorus laphygmae Vier.	Z	?	TX, NM, HI, northern S. America	1
	sp	Crops, weeds	TX	17
	Z	Alfalfa, sorghum	TX	18
	Z	?	TX	28
Microplitis brassicae (Mues.)	sp	Soybean	NC	38
Microplitis croceipes (Cresson)	V, Z	Crops, weeds	TX	17
	V, Z	Crops, & wild hosts	MS	8
	Z	Alfalfa, sorghum, cotton	AZ	25
	V, Z	Soybean	SC	22
	V, Z	Tobacco, cotton, soybean	SC	13
	V, Z	Cotton, sesame	MS	10

		Host	Location	Ref
	V, Z	Cotton	AR, TX, AZ	12, 15, 27
	Z	Peanut	OK	19
	V, Z	Crops	SC, AL	23, 14
	V, Z	?	USA, Northern Mexico	1, 28
	V, Z	Weeds	SC	23
	V, Z	Crops, weeds	TX	17, 18
	V, Z	Cotton, alfalfa	OK	21
	V, Z	Tobacco, tomato, weeds	MS	16
	sp	Alfalfa, cotton, sorghum, weeds	AZ	20
	Z	Soybean	NC	38
Microplitis melianae Vier.	Z	?	North-central USA, Ontario	1, 28
	Z	Alfalfa, sorghum	TX	18
	Z	Soybean	NC	38
Rogas perplexus Gahan	Z	?	AZ, CA, NM, TX	1, 28
	sp	Cotton	AZ	20
	Z	Alfalfa, corn, potato	TX	18
	Z	Soybean	NC	38
Zele mellea (Cresson)	Z	Alfalfa	TX	18
	A	Soybean	NC	38
Chalcididae				
Brachymeria ovata (Say)	Z	?	USA	28
	Z	Cotton	AZ	25
	Z	?	?	34
	Z	Soybean	NC	38

(continued)

Table 6 continued

ORDER Family Parasitoid	Species of Heliothis attacked	Host plant of Heliothis	Geographic range	Reference[a]
Brachymeria incerta (Cresson)	Z	?	FL, W. Indies, Mexico	33
Brachymeria robustus (Cresson)	Z	Soybean	NC	38
Cryptus albitarsis (Cresson)	Z	?	?	33
Spilochalcis femorata (Fabr.)	Z	Soybean	NC	38
Spilochalcis igneoides (Kirby)	Z	Cotton	Central America	3
	Z	?	Virgin Islands, USA	28, 34
Spilochalcis side (Walker)	Z	Soybean	NC	38
	V	?	?	34
Eulophidae				
Euplectrus comstockii Howard	sp	crops, weeds	TX	17
	Z	Alfalfa, cotton, potato	TX	18
	Z	?	?	34
	Z	?	USA	28
	Z	Soybean	NC	38
Euplectrus plathypenae Howard	Z	Peanut	OK	19
	sp	Crops, weeds	TX	17
	Z	?	?	34
	Z	?	Eastern USA	28
	Z	Soybean	NC	38
Ichneumonidae				
Campoletis argentifrons (Cress.)	Z	?	?	30
	Z	?	Uruguay	31
	Z	Cotton	CA	3
	Z	Soybean	NC	38
Campoletis flavicincta (Ashmead)	Z	Tomato	CA	7

Campoletis perdistinctus (Viereck)	Z	Soybean	SC	22
	V, z	Crops, weeds	SC	13, 23
	Z	?	USA	28
	V	Tobacco	NC	24
	Z	Soybean	NC	38
Campoletis sonorensis (Cameron)	V, z	Weeds, crops	SC	13, 23
	Z	Soybean	SC	22
	V, z	Cotton, sesame	MS	10
	Z	Peanut	OK	19
	V	Crops & wild hosts	MS	8
	V, z	Alfalfa, corn, cotton, potato, sorghum	TX	18
Campoletis websteri (Vier.)	sp	Crops, weeds	TX	17
Dusona laticincta (Cresson)	Z	Soybean	NC	38
Ecphoropsis perdistinctus Viereck	Z	?	Bolivia	6
Enicospilus concolor (Cresson)	Z	Soybean	NC	38
Hyposoter annulipes Cr.	Z	Cotton	CA	3
	Z	?	USA	28
	V	Tobacco	SC	13
Hyposoter exiguae (Vier.)	Z	Soybean	NC	38
	Z	Tomato	CA	7
	Z	Cotton	CA	3
	Z	?	NY, SC, CO, CA, HI, Saskatchewan	28
Hyposoter pilosulus (Provancher)	Z	Crops	AZ	25
Melobirus fuscifemora Graf	Z	Corn	CA	2

(continued)

Table 6 continued

ORDER Family Parasitoid	Species of Heliothis attacked	Host plant of Heliothis	Geographic range	Reference[a]
Nepiera fuscifemora Graf	Z	Tomato	CA	7
Netelia geminatus (Say)	Z	Soybean	NC	38
Netelia sayi (Cushman)	Z	?	USA, Mexico	28
Netelia spinipes (Cushman)	Z	Soybean	NC	38
	Z	?	USA, Mexico	28
Ophion ancyloneura Cam.	Z	Soybean	NC	38
Paniscus sp.	Z	?	Uruguay	31
Pristomerus pacificus appalachianus Vier.	Z	Cotton	Brazil	32
Pristomerus spinator (F.)	Z	Soybean	NC	38
	V, Z	Alfalfa, peanut	OK	21, 19
	Z	Tobacco, cotton	SC	13
	V, Z	Soybean	SC	22
	V, Z	Cotton, sesame	MS	10
	V	Crops	AZ	25
Sagarites sp	Z	Cotton	Brazil	32
Sagarites provancher (D.T.)	Z	?	Uruguay	31
Sinophorus eruficinctus (Walkley)	V, Z	Alfalfa, corn, cotton, potato, sorghum	TX	18
Therion californicum (Cress.)	Z	Cotton	CA	3
Scelionidae				
Telenomus heliothidis Ashmead	Z	?	LA, KS, TX, Cuba	28
	Z	Soybean	NC	38
Telenomus sp	V	Crops, wild plants	Colombia	9
Trichogrammatidae				
Trichogramma evanescens Westwood	Z	Soybean	NC	38

Trichogramma exiguum Pinto & Platner	sp	Corn, cotton	TX	35
Trichogramma maltbyi Nagaraja	sp	Corn, cotton	TX	35
Trichogramma minutum Riley	sp	Corn, cotton	TX	35
	sp	Corn, tomato, cotton	AL	14
	Z	Corn	Brazil	32
	V	?	Peru	36
	Z	?	?	34
	V, Z	Corn, cotton	SC	13
	Z	?	?	28
Trichogramma pretiosum Riley	Z	Soybean	NC	38
	Z	Tomato	CA	7
	sp	Corn, cotton	TX	35
	V	Crops, wild hosts	Colombia	9
DIPTERA				
Muscidae				
Muscina assimilis (Fallen)	Z	Cotton, soybean	NC	11, 38
	V	Cotton	SC	13
Muscina stabulans (Fallen)	Z	Cotton, soybean	NC	11, 38
Phoridae				
Megaselia (*Aphiochaeta*) *nigriceps* (Loew)	Z	Soybean	NC	38
Sarcophagidae				
Boettcheria latisterna Parker	Z	Soybean	NC	38
Helicobia rapax (Walker)	Z	Soybean	NC	38
Tachinidae				
Actinoplagia koehleri Blanchard	Z	?	Uruguay, Argentina, Chile	31, 37

Table 6 continued

ORDER Family Parasitoid	Species of *Heliothis* attacked	Host plant of *Heliothis*	Geographic range	Reference[a]
Archytas incertus (Macquart)	Z	Cotton	Brazil	32
Archytas marmoratus (Townsend)	Z	Cotton	AZ	25
	Z	Soybean	SC	22
	V, Z	Soybean, tobacco	NC	11, 38
	V, Z	Crops	AL	14
	V, Z	Crops, weeds	TX	17, 18
	sp	Alfalfa	OK	21
	V	Beggarweed	SC	23
	V, Z	?	N. America, W. Indies	37
	Z	Peanut	OK	19
	V, Z	Corn, beggarweed, soybean	SC	13
Archytas platonicus Cortes & Campos	Z	?	Peru	37
Archytas scutellatus (Macquart)	Z	?	Chile	37
Ateloglutus chilensis (Brethes)	Z	?	Chile	37
Athrycia cinerea (Coq.)	Z	?	N. America	37
Bonnetia compta (Fall.)	Z	?	N. America	37
Chaetogaedia analis (Walp)	Z	?	N. America	37
Chaetogaedia monticola (Bigot)	V, Z	?	N. America, HI	37
Chaetogaedia sp	V	Cotton	AZ	25
Chetogena (=*Euphorocera*) *claripennis* (Macquart)	Z	Alfalfa, corn, sorghum	TX	18
Chetogena floridensis (Townsend)	Z	Alfalfa, cotton	TX	18
Compsilura concinnata (Meigen)	Z	?	NJ	37
Eucarcelia illota Curran	Z	?	Bolivia	6

Eucelatoria armigera (Coquillet)	V, Z	Cotton	AZ, CA	25, 27, 3
	Z	Alfalfa, cotton	OK	21
	Z	Corn	CA	2
	sp	Corn, alfalfa, cotton, weeds	AZ	4
	Z	?	N. America	37
	Z	?	CA, AZ, Mexico	26
	Z	Peanut	OK	19
	Z	Soybean	NC	38
Eucelatoria australis Townsend	V, Z	?	Peru, Chile	37
Eucelatoria bryani Sabrosky	V, Z	Cotton	AZ	25
	V, Z	Crops	TX	18
	V, Z	?	AZ, KS, MS, MO, OK, TX, Mexico, C. America	26
Eucelatoria heliothis Sabrosky	V	Tobacco	Venezuela	26
	V	?	Honduras, Colombia	26
Eucelatoria rubentis (Coquillet)	Z	Soybean	SC	22
	Z	Corn	SC	13
	Z	Soybean	NC	11, 38
	Z	Morning glory	SC	23
Euphorocera floridensis Townsend	V, Z	?	NC, N. America, Bahamas, Mexico	26, 37
	Z	?	Uruguay	31
Euphorocera omissa (Reinhard)	Z	Peanut	OK	19
Euphorocera (=*Plagiotachina*)	sp	Alfalfa	OK	21
peruviana Townsend	V	?	Peru	36

(continued)

Table 6 continued

ORDER Family Parasitoid	Species of Heliothis attacked	Host plant of Heliothis	Geographic range	Reference[a]
Euphorocera tachinomoides Townsend	Z	Peanut	OK	19
	sp	Crops, weeds	TX	17
	Z	Alfalfa, sorghum	OK	21
	Z	?	AZ	25
Eusisyropa blanda (Coq.)	Z	Soybean	NC	38
Exorista mella (Walker)	Z	?	DE	37
Gonia capitata (Degeer)	Z	?	N. America	37
Gonia pallens Weidemann	Z	Cotton	CA	3
Goniophthalmus halli Mesnil	sp	?	Chile	37
Gymnochaetopsis fulvicauda (Walton)	Z	?	Bolivia	6
Hyphantrophaga hyphantriae (Tns.)	Z	?	W. Indies, Jamaica	37
	Z	?	AZ, TX	25, 37
Incamyia charlini Cortes	Z	Soybean	NC	38
Incamyia spinicosta Ald.	Z	?	Chile	37
Lespesia aletiae (Riley)	Z	?	Argentina, Chile	37
	Z	Soybean	SC	22
	V, Z	Soybean, peanut, cotton	SC	13
	Z	Soybean	NC	11, 38
	Z	Peanut	OK	19
	V, Z	Crops, morning glory	SC	23
	V, Z	Beggarweed	N. America	37
Lespesia (=Achaetoneura) archippivora (Riley)	Z	Soybean	SC	22
	Z	Cotton, sesame	MS	10
	Z	Peanut	OK	19
	sp	Crops, weeds	TX	17

Species		Host	Location	References
	Z	Alfalfa, cotton	OK	21
	Z	Corn, cotton	CA	2, 3
	Z	Cotton, alfalfa, corn, sorghum	AZ	4, 25, 27
Lespesia frenchii (Will.)	Z	?	N. America	37
	V, Z	Alfalfa, cotton, sorghum	TX	18
	Z	Soybean	NC	38
	Z	?	N. America	37
Metaplagia occidentalis Coq.	V, Z	Soybean	NC	38
Metavoria orientalis Tns.	Z	?	N. America	37
Myiosturmia mixta Tns.	V	?	N. America	37
Nemorilla floralis (Fallen)	Z	?	Brazil	37
Nemorilla pyste (Walk.)	Z	Soybean	NC	38
	Z	?	N. America, Virgin Islands	37
	Z	Soybean	NC	38
Peleteria pigmaea (Macq.)	Z	?	Argentina, Brazil, Chile	37
Plagiomima cognata Ald.	sp	Alfalfa	AZ	4
Plagiomima spinosula (Bigot)	Z	Corn	OK	21, 37
Siphona plusiae Coq.	Z	Tomato	CA	2, 7, 37
Spallanzania hebes (Fallen)	Z	Soybean	NC	38
Spogosia claripennis (Macq.)	V, Z	?	N. America	37
Spogosia floridensis (Tns.)	V, Z	?	N. America	37
Spogosia omissa (Rein.)	Z	?	N. America	37
Spogosia peruviana (Tns.)	V	?	Peru	37
Spogosia tachinomoides (Tns.)	Z	?	N. America	37

(continued)

Table 6 continued

ORDER Family Parasitoid	Species of Heliothis attacked	Host plant of Heliothis	Geographic range	Reference
Voria aurifrons (Townsend)	Z	Peanut	OK	21, 27
	Z	Soybean	NC	38
Voria ruralis (Fallen)	sp	Crops, weeds	TX	17
	Z	?	OK	37
Winthemia quadripustulata (Fab.)	Z	Cotton	CA	3
	Z	Soybean	NC	38
Winthemia rufopicta (Bigot)	Z	Soybean	SC	22
	V, Z	Soybean, tobacco	NC	11, 38
	V	Tobacco	SC	13
Winthemia sinuata Reinhard	V, Z	Alfalfa	OK, N. America	21, 37
	V, Z	Peanut	OK, N. America	19, 37

[a] References

1. Marsh 1978.
2. Oatman & Platner 1970.
3. van den Bosch & Hagen 1966.
4. Butler 1958a.
5. Bennett & Yaseen 1972.
6. Bennett & Squire 1972.
7. Oatman et al. 1983.
8. Stadelbacher et al. 1984.
9. Hallman 1980.
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11. Hughes 1974.
12. Burleigh & Farmer 1978.
13. Roach 1976.
14. Watson et al. 1966.
15. Shepard & Sterling 1972.
16. Lewis & Brazzell 1968.
17. Harding 1976.
18. Puterka et al. 1985.
19. Wall & Berberet 1975.
20. Butler 1958b.
21. Bottlrell et al. 1968.
22. McCutcheon & Turnipseed 1981.
23. Roach 1975.
24. Rabb et al. 1955.
25. Butler et al. 1982.
26. Sabrosky 1981.
27. Bryan et al. 1969.
28. Muesbeck et al. 1951.
29. Ayala Sifontes et al. 1982.
30. Krombein 1958.
31. Silveira Guido & Ruffinelli 1956.
32. Costa Lima 1948.
33. Krombein & Burks 1967.
34. Peck 1963.
35. Lopez et al. 1982.
36. Beingolea 1955.
37. Sabrosky 1978.
38. Deitz et al. 1976.

[b] Abbreviations of U.S. state names in order of occurrence in the table: CA = California; TX = Texas; SC = South Carolina; NC = North Carolina; AZ = Arizona; GA = Georgia; LA = Louisiana; FL = Florida; KS = Kansas; MS = Mississippi; AR = Arkansas; AL = Alabama; OK = Oklahoma; NM = New Mexico; HI = Hawaii; CO = Colorado; NJ = New Jersey; MU = Missouri; DE = Delaware.

Table 7. Number of papers on major parasitoids of Heliothis *spp. in the USA*

Species	Number of papers
Cardiochiles nigriceps	118
Microplitis croceipes	91
Cotesia (Apanteles) marginiventris	81
Trichogramma spp.	49
Archytas marmoratus	26
Meteorus autographae	23
Pristomerus spp	18
Lespesia aletiae	17
Winthemia rufopicta	12
Bracon mellitor	9
Telenomus heliothidis	7
Brachymeria spp.	5

shown to prey directly on a specific life stage of *Heliothis* spp. were included. Accounts of predatory species collected in association with *Heliothis* populations in the course of insecticide evaluations or similar studies were ignored for the purpose of this compilation. The resulting list of 141 species of predaceous arthropods were most often found affecting *Heliothis* populations on cotton; however, these species are by no means limited in occurrence to this crop. More likely, this is merely a reflection of the research effort directed toward a better understanding of natural controls in cotton.

The predominant groups of predaceous arthropods include Coleoptera (especially Coccinellidae), Hemiptera (especially Nabidae), Hymenoptera (especially Formicidae), and Araneida. Nearly 90% of the recorded predators of *Heliothis* spp. belong to these four orders. Some additional indication of the relative importance of particular predator species can be deduced from the number of papers listed in Table 9. It is generally thought that predators, such as those that feed on eggs or early instars of *Heliothis*, are most important in preventing the buildup of damaging populations. Those that feed on late instars may be somewhat important in reducing numbers of the large larvae, but the effects may not be observed until pest populations are already high, and damage to the crop has already occurred. Detailed accounts of the relative abundance and importance of specific predators in various locations are found in most of the references included in this checklist.

Table 8. Checklist of predators of Heliothis virescens and H. zea in North, Central, and South America, and life stage attacked
(E = egg; L = larva; P = pupa; A = adult)

ORDER Family Predator	Life stage attacked	Host plant of *Heliothis*	Geographic range	Reference[a]
COLEOPTERA				
Anthicidae				
Notoxus calcaratus Horn	E	Cotton	AZ[b]	5
Cantharidae				
Chauliognathus marginatus Fabr.	L	Corn	USA	20
Chauliognathus pennsylvanicus DeGeer	L	?	USA	20
Carabidae				
Calosoma externum Say.	L, A	Cotton	AR	10
Calosoma retusum Fabr.	?	?	Uruguay	14
Calosoma sayi Dej.	L, P, A	Cotton	AR	10, 17
Calosoma scrutator Fabr.	L, A	Cotton	AR	10, 18
Geopinus incrassatus (Dej.)	L	Cotton	AR	16
Lebia analis Dej.	E, L	Cotton	AR	4, 10, 18
Cicindelidae				
Cicindela peruviana Lap.	L	Corn, cotton	Peru	3
Tretracha chilensis Cart	L	Corn, cotton	Peru	3
Coccinellidae				
Ceratomegilla fuscilabris Muls.	L	Corn	USA	20
Ceratomegilla maculata (DeGeer)	L	Corn, cotton	Peru	3
Coccinella novemnotata Herbst	E, L	Cotton	AR	4, 10, 16, 18
Coleomegilla fuscilabris (Muls.)	E	Cotton	TX	6
Coleomegilla maculata (DeGeer)	E, L	Cotton	Southern USA	14
	?	Cotton	MS. Delta	15
	E, L	Cotton	AR	4, 10, 16, 17, 18

Species	Stage	Crop	Location	References
Cycloneda sanguinea (L.)	E, L	Cotton	AR	17
Eriopis convexa Germ.	L	Corn, cotton	Peru	3
Hippodamia convergens Guérin	L	Corn, cotton	Peru	3
	E, L	Cotton	TX	1, 6, 11, 12
	L	Corn	USA	20
	E, L	Cotton	Southern USA	13
	E	Cotton	AZ	5
	E, L	Cotton	AR	4, 10, 17, 18
	L	Corn, cotton	Peru	3
Scymnus americanus Muls.	E	Cotton	AR	4
Scymnus creperus Muls.	E	Cotton	TX	6
Scymnus fraternus Leconte	E	Cotton	AR	4, 10
Scymnus hortensis Wingo	E	Cotton	AR	4
	E, L	Cotton	TX	11
Scymnus loweii Mulsant	E, L	Cotton	TX	11
Scymnus rubricaudus Casey	E	Cotton	AR	4
Scymnus terminatus Say	E	Cotton	AR	4
Lathridiidae				
Melanophthalma distinguenda (Com.)	E	Cotton	TX	6
Melyridae				
Collops balteatus Leconte	E, L	Cotton	TX	6, 11, 12
Collops quadrimaculatus Fabr.	E, L	Cotton	AR	4, 10, 16, 18
	E, L	Cotton	AR	4, 10, 16
Collops vittatus (Say)	E, L	Cotton	TX	11
	E	Cotton	AZ	5

(continued)

Table 8 continued

ORDER Family Predator	Life stage attacked	Host plant of *Heliothis*	Geographic range	Reference[a]
DIPTERA				
Asilidae				
Deromyia angustipennis (Loew.)	A	?	TX	20
Erax interruptus Macq.	A	Cotton	Southern USA	20
HEMIPTERA				
Anthocoridae				
Orius insidiosus (Say)	E, L	Corn	USA	20
	E, L	Cotton	Southern USA	13
	E, L	Cotton	TX	1, 6, 11, 12
	?	Cotton	MS Delta	15
	E	Cotton	AZ	18
	E, L	Corn, cotton	Brazil	8
Orius tristicolor (White)	E, L	Cotton	Southern USA	13
	E	Cotton	AZ	5
	E, L	Corn, cotton	Peru	3
Paratriphleps laeviusculus Champ.	E, L	Corn, cotton	Peru	3, 7
Berytidae				
Parajalysus spinosus Dist.	E, L	Corn, cotton	Peru	3
Coreidae				
Acanthocephala femorata Fabr.	L	Cotton	Southern USA	20
Lygaeidae				
Geocoris pallens	E	Cotton	AZ	5
Geocoris punctipes (Say)	E, L	Cotton	TX	1, 6, 11, 12
	E	Cotton	AZ	5
	E, L	Cotton	AR	16, 18
	E, L	Cotton	Southern USA	13

Species	Stage	Crop	Location	Ref.
Geocoris uliginosus (Say)	L	Corn	Southern USA	20
	E, L	Corn, cotton	Peru	3
	E, L	Cotton	TX	11
Hypogeocoris imperialis (Distant)	E, L	Cotton	AR	18
Hypogeocoris piceus (Say)	E, L	Cotton	AR	18
Miridae				
Cyrtopeltis tenuis Reuter	E, L	Tobacco	Cuba	2
Cyrtopeltis varians Dist.	E, L	Tobacco	Cuba	2
	E, L	?	FL, TX	20
Deraeocoris nebulosus (Uhler)	E	Cotton	AR	10
Hyalochloria denticornis Tsay-Yu Hsiac	E, L	Corn, cotton	Peru	3
Macrolophus praeclarus (Distant)	E, L	Tobacco	Cuba	2
Pseudatomoscelis seriatus (Reuter)	E	Cotton	TX	12
Rhinacloa carmelitana Carvalho	E, L	Corn, cotton	Peru	3
Spanogonicus albofasciatus (Reuter)	E	Cotton	AZ	5
Nabidae				
Nabis alternatus (Parshley)	E, L	Cotton	Southern USA	13
	E, L	Cotton	TX	11
	E, L	Cotton	AR	10, 18
Nabis capsiformis Germar	E, L	Cotton	AR	10, 18
Nabis deceptivus Harris	E, L	Cotton	AR	18
Nabis ferus (L.)	L	Corn	USA	11
	E	Cotton	AZ	5
	E, L	Cotton	Southern USA	13
	E, L	Cotton	AR	10, 18

Table 8 continued

ORDER Family Predator	Life stage attacked	Host plant of Heliothis	Geographic range	Reference[a]
Nabis punctipennis Blanch.	E, L	Corn, cotton	Peru	3, 8
Nabis pseudopunctipennis	E, L	Corn, cotton	Peru	7
Nabis roseipennis Reuter	E, L	Cotton	AR	18
Nabis sordidus Reuter	E, L	Cotton	AR	18
Pentatomidae				
Podisus maculiventris (Say)	E	Cotton	TX	6
	L	Cotton	AR	10, 18
Podisus spinosus Dalt.	L	?	USA	20
Reduviidae				
Arilus cristatus (L.)	L, A	Cotton	AR	10, 18
Sinea diadema (Fabr.)	E, L	Cotton	AR	4, 10
Sinea spinipes (Herrich-Schaeffer)	E, L	Cotton	AR	4, 10
Zelus cervicalis (Stal)	L	Cotton	AR	**10, 18**
Zelus exsanguis (Stal)	L	Cotton	AR	10, 18
Zelus renardii Kolenat	E, L	Cotton	TX	6, 11
Zelus socius Uhl.	E	Cotton	TX	6
	L	Cotton	AR	**10, 18**
HYMENOPTERA				
Formicidae				
Camponotus socius Roger	L	Soybean	FL	19
Canomyrma pyramicus (Roger)	E	Soybeans	FL	19
Doromyrmex pyramicus (Roger)	L	Cotton	Southern USA	20
Forelius foetidus (Buckley)	L	Cotton	AR	16
Iridomyrmex pruinosus (Roger)	E, L	Cotton	AR	10, 16, 17, 18
Iridomyrmex pruinosus analis (Andre)	L	Cotton	AR	16
Lasius neoniger Emery	L	Soybean	FL	16
Lasius niger americanus Emery	L	?	IL	19
Monomorium carbonarium Smith	E, L	Cotton	Southern USA	20

Monomorium minimum (Buckley)	L	Cotton	AR	10, 18
Monomorium viridum Brown	L	Soybean	FL	19
Pheidole bicarinata Mayr.	L	Cotton	AR	16
Pheidole bicarinata longula Emery	L	Cotton	AR	15
Pheidole bicarinata vinelandica Forel	E, L	Cotton	AR	10, 16
Solenopsis geminata Fab.	E, L	?	USA	20
	L	Soybean	FL	19
Solenopsis invicta Buren	E	Cotton	TX	12
	L	Soybean	FL	19
Solenopsis molesta Say	E, L	?	USA	20
	E, L	Cotton	AR	10
Solenopsis texana Emery	L	?	TX	20
Vespidae				
Eumenes bolli Cress.	L	?	TX	20
Polistes annularis (L.)	L	?	USA	20
	L	Cotton	AR	10, 18
Polistes cubensis Lepeletier	L	Tobacco	Cuba	2
Polistes exclamans Vier.	L	Cotton	AR	10, 18
Polistes fuscatus (Fabr.)	L	Cotton	AR	10, 16, 18
Polistes hunteri Bequaert	L	Cotton	AR	10, 18
Polistes metricus Say	L	Cotton	AR	10, 18
Polistes rubiginosus Lepeletier	L	?	USA	20
	L	Cotton	AR	10, 16, 18
Polistes texanus Cress.	L	?	TX	20
Vespula squamosa (Drury)	L	Cotton	AR	16

Table 8 continued

ORDER Family Predator	Life stage attacked	Host plant of *Heliothis*	Geographic range	Reference[a]
LEPIDOPTERA				
Noctuidae				
Heliothis zea (Boddie)	L (cannibalism)	Cotton	AR	16
NEUROPTERA				
Chrysopidae				
Chrysopa carnea Stephens	E	Cotton	AZ	5
	E, L	Cotton	TX	1, 11
	E, L	Cotton	Southern USA	13
Chrysopa harrisii Fitch	E	Cotton	AR	10, 18
Chrysopa intacta Navas.	E	Cotton	AR	18
Chrysopa nigricornis Burmeister	E	Cotton	AR	18
Chrysopa oculata Say	E	Cotton	AR	10, 18
	E, L	Cotton	Southern USA	13
	E, L	Corn	USA	20
Chrysopa plorabunda Fitch	E, L	Corn	USA	10, 20
Chrysopa quadripunctata Burmeister	E	Cotton	AR	18
Chrysopa rufilarris Burmeister	E, L	Cotton	TX	6, 11
	E, L	Cotton	Southern USA	13,
	E	Cotton	AR	10, 18
ODONATA				
Libellulidae				
Erythemis simplicollis (Say)	A	Cotton	AR	4, 10, 17
ORTHOPTERA				
Gryllidae				
Oecanthus nigricornis Walker	E	?	AR	18

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Mantidae				
Stagmomantis carolina (Johannson)	A	Cotton	AR	18
Tettigoniidae				
Conocephalus fasciatus (DeGeer)	L	Cotton	AR	16, 18
Orchelimum vulgara Harris	E	Cotton	AR	18
ACARINA				
Erythraeidae				
Balaustium dowelli Smiley	E	Cotton	AR	10, 17
Erythremis whitcombi Smiley	E	Cotton	AR	10, 17
ARANEIDA				
Anyphaenidae				
Aysha gracilis (Hentz)	E	Cotton	TX	12
Argiopidae				
Acanthapeira stalli (Walck.)	L, A	Cotton	AR	10, 16, 18
Argiope aurantia Lucas	L	Cotton	TX	9
Neoscona arabesca (Walck.)	A	Cotton	AR	10, 18
Neoscona sacra (Walck.)	A	Cotton	AR	10, 18
Tetragnatha laboriosa Hentz	L	Cotton	AR	16
Clubionidae				
Chiracanthium inclusum (Hentz)	E	Cotton	TX	12
Dictyonidae				
Dictyona bellans Chamberlin	E	Cotton	AR	10
Erigonidae				
Grammonota texana (Banks)	L	Cotton	AR	, 16
Gnaphosidae				
Cylphosa sericata (L. Koch)	L	Cotton	AR	16

(continued)

Table 8 continued

ORDER Family Predator	Life stage attacked	Host plant of *Heliothis*	Geographic range	Reference[a]
Lycosidae				
Lycosa annexa Chamberlin & Ivie	A	Cotton	AR	10
Lycosa carolinensis Walck.	L, A	Cotton	AR	16
Lycosa helluo Walck.	L, P	Cotton	AR	10
Lycosa rabida Walck.	P, A	Cotton	AR	10, 18
Pardosa milvina (Hentz)	L	Cotton	AR	10, 16
Schizocosa avida Walck.	A	Cotton	AR	10
Oxyopidae				
Oxyopes apollo Brady	L	Cotton	AR	16
Oxyopes salticus Hentz	L	Cotton	Southern USA	13
	E, L	Cotton	TX	11, 12
	L	Cotton	AR	10, 16
Peucetia viridans (Hentz)	L, A	Cotton	AR	10, 18
Salticidae				
Habronattus coronatus (Hentz)	E	Cotton	AR	10
Hentzia palmarum (Hentz)	L	Cotton	AR	16
Metaphidippus galathea (Walck.)	E, L	Cotton	AR	10, 16
Metaphidippus protervus (Walck.)	L	Cotton	AR	10
Phidippus audax (Hentz)	E	Cotton	TX	12
	L	Cotton	AR	10
Phidippus carolinensis Peckham & Peckham	L	Cotton	AR	10
Phidippus clarus Keyserling	L	Cotton	AR	10
Phidippus variegatus (Lucas)	L, A	Cotton	AR	10, 18
	L	Cotton	TX	9
Theridiidae				
Archaearanea tepidariorum (C.L. Koch)	L	Cotton	AR	10

Species				
Theridion australe Banks	L	Cotton	AR	10
Thomisidae				
Misumenoides aleatorius (Hentz)	L	Cotton	AR	10, 15
Misumenops celer (Hentz)	L	Cotton	TX	9
	L	Cotton	TX	9
Misumenops oblongus (Keyserling)	L	Cotton	AR	16

[a]References

1. Ables et al. 1978.
2. Ayala Sifontes et al. 1982.
3. Beingolea 1955.
4. Bell & Whitcomb 1964.
5. Butler 1966.
6. Ewing & Ivy 1943.
7. Gaviria 1952.
8. Hambleton 1944.
9. Kogan 1943.
10. Lincoln et al. 1967.
11. Lingren et al. 1968.
12. McDaniel & Sterling 1982.
13. Ridgeway & Lingren 1972.
14. Silveira Guido & Ruffinelli 1956.
15. Smith & Stadelbacher 1978.
16. Whitcomb 1967.
17. Whitcomb 1974.
18. Whitcomb & Bell 1964.
19. Whitcomb et al. 1972.
20. Winburn & Painter 1932.

[b] Abbreviations of U.S. state names in order of occurrence in the Table: AZ = Arizona; AR = Arkansas; TX = Texas; MS = Mississippi; FL = Florida.

Table 9. Number of papers on major predators of Heliothis *spp. in North, Central, and South America*

Species	Number of papers
Geocoris	286
Chrysopa	271
Orius	265
Nabis	232
Hippodamia convergens	178
Collops	97
Coleomegilla maculata	92
Podisus	85
Polistes	71
Scymnus	65

DISCUSSION AND CONCLUSIONS

The losses caused by *Heliothis virescens* and *H. zea* to all crops have never been exactly assessed, but they probably run into the hundreds of millions annually. These species in the USA are not only the most important pests of cotton, tobacco, and tomato, but are now considered the most important pest of soybean, as well (Kogan 1980). More research is done on *Heliothis* spp. each year than on any other pest species of field or vegetable crops. Despite this research effort, control of *Heliothis* in most crops is achieved mainly by application of insecticides. We have searched the SIRIC database for the papers on *H. virescens* and *H. zea* coded also for each of the four major control methods, and have obtained these results: 2046 papers were also coded for chemical control, 769 for biological control, 697 for plant resistance, and 618 for cultural control. Nearly as many papers were coded for chemical control as for the other three methods combined. It is apparent that if numbers of papers reflect research effort, chemical control receives almost three times the effort devoted to biological control. At present, although plant resistance and biological control are important tactics in the management of *Heliothis* spp. on various crops, they alone cannot prevent populations from reaching the economic injury level in most years on most crops.

The fact that *H. zea* and *H. virescens* are native to the New World makes them less viable candidates for successful biological control. However, *H. virescens* has been a classic example of a pest created by the disruption of natural controls through the indiscriminate use of insecticides. Is it possible to reverse this process? A better understanding of the role of natural agents in the regulation of *Heliothis* spp. populations is likely to help. The importation and colonization of natural enemies that

attack *Heliothis* spp. elsewhere in the world is another avenue that needs additional exploitation (Clausen 1978).

The SIRIC database provided also a basis for a bibliometric analysis of the *Heliothis* literature. In general, there is remarkable agreement between the assessment of importance of specific predators or parasitoids based on the bibliometric analysis and assessments provided by various authors. Despite the considerable research effort that has been invested in *Heliothis* spp., there is a dire need to conduct systematic surveys of natural enemies, with emphasis on detailed records of the host plant (three-trophic level associations) and the *Heliothis* growth stage that is attacked (age-specific predation or parasitism). It is also imperative to develop uniform criteria to assess the effectiveness of specific natural enemies. As new varieties of crop plants are developed, some with increased levels of resistance to *Heliothis*, it will be essential to assess the interactions of resistance with biological control. To perform these surveys it is necessary to have the best possible taxonomic support to guarantee correct identifications and to clarify synonymies. Finally, this paper stresses a grossly overlooked facet of research: information management. Information accumulates at a rate that exceeds human ability to absorb and to put to use. We suggest that more support be given to promote and coordinate efforts that make information more efficiently available to the various levels of the user community. This conference, and the papers in these proceedings, are a step in the right direction.

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Distribution and Economic Importance of *Heliothis* spp. and Their Natural Enemies and Host Plants in Southeast Asia

Banpot Napompeth*

ABSTRACT

In most southeast Asian countries, taxonomic studies on *Heliothis* spp. are limited. Only *H. armigera* (Hübner) and *H. assulta* are known and both are of economic importance on major crops such as corn, cotton, tobacco, and other crops. These two species are distributed throughout the southeast Asian region and in other geographical regions as well. *H. armigera* has a longer list of host plants and of reported natural enemies than *H. assulta*. Natural enemies reported could attack both *Heliothis* spp., and various attempts have been made to exploit these natural enemies in integrated pest management programs for these important pests.

Geographically, southeast Asia covers part of the land area of continental Asia and the insular area bridging the Indian and Pacific Oceans. Countries considered within the southeast Asian region are: Brunei, Burma, Indonesia, Kampuchea, Laos, Malaysia, Philippines, Singapore, Thailand, and Vietnam. Within this region, *Heliothis* spp. and their systematics are yet to be investigated and taxonomic studies carried out. More extensive and intensified surveys might reveal a large number of *Heliothis* spp. distributed in the southeast Asian region. At present, however, most research and studies on *Heliothis* spp. in southeast Asia are limited to *Heliothis armigera* (Hübner) and *H. assulta* Guenée. Both species are of obvious economic importance in almost all countries of southeast Asia (CIE 1968, 1969; Hill 1975; Krantz et al. 1977). These *Heliothis* spp. are sometimes reported in the literature as *Helicoverpa* spp. in some countries such as the Philippines and Thailand (Areekul et al. 1970; Esguerra and Gabriel 1969; Mabbett el al. 1979; Schmutterer 1978; Supharngkasen

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1979), or *Chloridea* spp. in Burma and Malaysia (Ghosh 1940; Yunus and Balasubramaniam 1975).

The purpose of this paper is to collate available information pertinent to biological control of *Heliothis* spp. in southeast Asia, with emphasis on the distribution and economic importance, listing of host plants of various *Heliothis* spp., and assessment of the importance of their natural enemies, for possible use of biological control as one basic component in the integrated pest management system for *Heliothis* spp.

DISTRIBUTION OF *HELIOTHIS* SPP.

Geographical distribution of both *H. armigera* (CIE 1968) and *H. assulta* (CIE 1969) covers the whole range of southeast Asian countries and extends to other geographical regions in the Old World. *H. armigera* has a much wider distribution than *H. assulta*, which is restricted to the Old World only.

ECONOMIC IMPORTANCE

Both *H. armigera* and *H. assulta* cause serious damage to crops of major and minor economic importance in their areas of distribution. However, the extent of damage inflicted by these pests varies widely, ranging from negligible damage all the way to total crop loss in many instances, and such a variation in terms of damage is also characteristic of *Heliothis* spp. The origin of infestation also varies greatly in different countries. In some countries the pests had long been observed but the intensity of damage caused remained insignificant and relatively unchanged. Recently, however, infestation has spread so rapidly that they have become dominant key pests and control through scheduled chemical application has become a standard practice.

The economic importance of *H. armigera* in southeast Asia in general was reported by Hill (1975) and together with *H. assulta* by Krantz et al. (1977). Various authors have reported on the extent of damage to certain crops in certain countries within the region, the host plants, and the occurrence of natural enemies of *Heliothis* spp. It is obvious from such reports that the conventional application of pesticides has been normally recommended for the control of these *Heliothis* spp.

HOST PLANTS OF *H. ARMIGERA* AND *H. ASSULTA*

H. armigera has a much wider host range than *H. assulta*. All known records of host plants of *H. assulta* include the same crops or plants that

Table 1. **Host plants** of Heliothis *spp.* *in Southeast Asian countries*

| Country and species | Host plant | |
	Common name	Scientific name
BRUNEI	(No report available)	
BURMA		
H. armigera	Chickpea	*Cicer arietimum*
	Beans	—
	Peas	*Pisum sativum*
H. assulta	Tobacco	*Nicotiana tabacum*
INDONESIA		
H. armigera	Castor	*Ricinus communis*
	Maize	*Zea mays*
	Cotton	*Gossypium* spp.
	Flax	*Linum usitatissimum*
	Green manures	—
	Mimosa	*Mimosa invisa*
	Oats	*Avena sativa*
	Ornamentals	—
	Potato	*Solanum tuberosum*
	Pulses	—
	Sorghum	*Sorghum bicolor*
	Tobacco	*Nicotiana tabacum*
	Vegetables	—
H. assulta	Tobacco	*Nicotiana tabacum*
	Wild tobacco	*Nicotiana* sp.
	Gooseberry	*Physalis angulata*
	Castor	*Ricinus communis*
KAMPUCHEA		
Heliothis sp.	Maize	*Zea mays*
	Cotton	*Gossypium* spp.
	Peanut	*Arachis hypogaea*
	Tomato	*Lycopersicon esculentum*
LAOS	(No report available)	
MALAYSIA		
H. armigera	Tomato	*Lycopersicon esculentum*
H. assulta	Tobacco	*Nicotiana tabacum*
PHILIPPINES		
H. armigera	Bean	—
	Maize	*Zea mays*

Country and species	Host plant	
	Common name	Scientific name
	Cotton	*Gossypium* spp.
	Crucifers	—
	Egg plant	*Solanum* sp.
	Mungbean	*Phaseolus radiatus*
	Pepper	*Piper nigrum*
	Sorghum	*Sorghum bicolor*
	Tobacco	*Nicotiana tabacum*
	Tomato	*Lycopersicon esculentum*
SINGAPORE	(No report available)	
THAILAND		
H. armigera	Maize	*Zea mays*
	Cotton	*Gossypium* spp.
	Kenaf	*Hibiscus cannabinus*
	Mungbean	*Phaseolus radiatus*
	Okra	*Abelmoschus esculentus*
	Soybean	*Glycine max*
	Tobacco	*Nicotiana tabacum*
	Tomato	*Lycopersicon esculentum*
	Wild plants in the families: Convolvulaceae, Cucurbitaceae, Gramineae, Leguminosae, Malvaceae, and Solanaceae. 20 species of ornamentals in highland agriculture.	
H. assulta	Soybean	*Glycine max*
	Tobacco	*Nicotiana tabacum*
	Tomato	*Lycopersicon esculentum*
	Wild solanaceous plants	
VIETNAM		
H. armigera	Maize	*Zea mays*
	Cotton	*Gossypium* spp.
H. assulta	Tobacco	*Nicotiana tabacum*

also serve as host plants for *H. armigera* but not vice versa. In tobacco, where *H. assulta* should be the dominant species, it is very common to find a mixed population that includes *H. armigera*.

As Table 1 shows, no information on host plants of *H. armigera* and *H. assulta* is available from Brunei, Laos, and Singapore, but we may assume that the host plants will be similar to, or even the same as, those reported from other adjacent southeast Asian countries. Records on host plants of *Heliothis* spp. from various countries are as follows:

Country	Reference
Burma	Ghosh (1940); Napompeth (1981a)
Indonesia	Van Der Laan (1981)
Kampuchea	Nickel (1979)
Malaysia	Yunus and Balasubramaniam (1975)
Philippines	Esguerra and Gabriel (1969); Litsinger et al. (1978); Schmutterer (1978)
Thailand	Areekul et al. (1970); DOA (1965) Lippold (1973); Mabbett (1983); Napompeth (1966, 1981c, 1985); NBCRC (1976); Sinchaisri (1985); Tirawat and Wongsiri (1975); Wongsiri (1983)
Vietnam	Ho Khac Tin (1982); Luu Than Muu et al. (1981); Napompeth (1983, 1984); Vu Cong Hau (1978)

NATURAL ENEMIES OF *H. ARMIGERA* AND *H. ASSULTA*

It is obvious from the literature that natural enemies of *H. armigera* and *H. assulta* in southeast Asian countries are limited and less extensively distributed than the pest. Reports on natural enemies of *H. assulta* are almost nonexistent; any that are reported are together with those of *H. armigera* (e.g., Wongkobrat et al. 1985, from Thailand). It is certain, however, that most natural enemies—parasites, predators, and pathogens—to a large extent attack both species, at least in this part of the world. It is also possible that more effort has been spent on investigating natural enemies of *H. armigera*; thus a relatively longer list has been compiled. Also, as is the case with a list of host plants of *Heliothis* spp., no report or information is available on the principal natural enemies of *Heliothis* spp. (Table 2)

Table 2. Principal natural enemies of Heliothis *spp. in Southeast Asian countries*

Country and species	Natural enemy	*Heliothis* stage attacked
BRUNEI	(No report available)	
BURMA	(No report available)	
INDONESIA		
H. armigera	*Trichogramma nana* (Zehntn.)	Egg
	Eriborus argenteopilosus (Cam.)	Larva
	Tachinids	Larva

Country and species	Natural enemy	*Heliothis* stage attacked
	Metarhizium	Larva
	Nematodes	Larva
H. assulta	*Trichogramma* sp.	Egg
KAMPUCHEA	(No report available)	
LAOS	(No report available)	
MALAYSIA	(No report available)	
PHILIPPINES		
H. armigera	*Trichogramma* sp.	Egg
H. assulta	*Microplitis manilae*	Larva and pupa
	Eumenes campaniformis	Larva
	Eumenes pyriformis philippinensis	Larva
	Capsid bug	Egg
	Mirid bug	Egg
	Bacterial disease	Larva
	Virus disease	Larva
SINGAPORE	(No report available)	
THAILAND		
H. armigera		
Parasites	*Trichogramma confusum* Viggiani	Egg
	Trichogrammatoidea bactrae Nagaraja	Egg
	Carcelia rutilla Rondani	Larva
	Erioborus argentiopilosus	Larva
	Exorista sorbillans Wiedemann	Larva
	Phorcida sp.	Larva
Predators	*Ankylopteryx* sp.	Larva
	Ankylopteryx octopunctata	Larva
	Chlaenius sp.	Larva
	Chrysopa basalis Walker	Larva
	Chrysopa ochracea	Larva
	Coccinella repanda Thunberg	Larva
	Eocanthecona furcellata (Wolff)	Larva
	Eumenes sp.	Larva
	Geocoris sp.	Larva
	Harpactor tristicolor Reuter	Larva
	Harmonia arcuata F.	Larva
	Heirodula bipapilla	Larva
	Macranthopsis nodipes Reuter	Larva
	Menochilus sexmaculata (F.)	Larva
	Nabis sp.	Larva
	Nabis ferus (L.) ?	Larva
	Oecophylla smaragdina F.	Larva

	Ophionea indica Thunberg	Larva
	Ropalidia sp.	Larva
	Ropalidia fasciata	Larva
	Ropalidia guttatipennis Sauss.	Larva
	Sycanus collaris F.	Larva
	Veronia discolor (F.)	Larva
Pathogens	Nuclear Polyhedrosis Virus	Larva
H. assulta	No natural enemy has been reported from *H. assulta* in Thailand. Those reported are from mixed populations of *H. armigera* and *H. assulta*	
VIETNAM		
H. armigera	*Trichogramma chilonis*	Egg
	Apanteles kazak	Larva
	Habobracon hebetor	Larva

from Brunei, Burma, Kampuchea, Laos, Malaysia, and Singapore. Again, we may assume that the natural enemies are similar to, or the same as, those reported from adjacent areas or countries, for many have also been reported from regions outside or adjacent to southeast Asia.

Records of natural enemies of *Heliothis* spp. from various southeast Asian countries are as follows:

Country	Reference
Indonesia	Van Der Laan (1981)
Philippines	Baltazar (1980); Esguerra and Gabriel (1969); Schmutterer (1978)
Thailand	Hungspruke et al. (1981); Messenger (1973a, 1973b, 1973c); Nanta and Pathomrat (1976); Nanta et al. (1981) Napompeth (1981b, 1982); NBCRC (1976); Supharngkasen (1979); Wongkobrat et al. (1985)
Vietnam	Ho Khac Tin (1982); Napompeth (1983, 1984)

DISCUSSION

Attempts to launch biological control programs for *Heliothis* spp. in southeast Asia in most cases have been confined to the exploration and evaluation of natural enemies associated with them. When certain natural enemies or any promising biological control agents were found, recommendations were made, but in most cases only limited work could be accomplished or, if accomplished, was of hardly any practical use. In

Thailand, Messenger (1973) suggested the procedures for conducting a biological control program against *H. armigera* and recommended introduction of *Microplitis croceipes* (Cresson), a parasite of *H. zea* (Boddie), *Campoletis sonorensis* (Cameron), and *Cardiochiles nigriceps* Viereck from the USA. However, such recommendations were never put into active practice. Deema et al. (1974) also advocated an integrated pest management program. The lacewing, *Chrysopa basalis* Walker was a predator utilized (Nanta and Pathomrat 1976). Attempts were also made to use a crude preparation of nuclear polyhedrosis virus (NPV) to control *H. armigera* in Thailand (Hungspruke et al. 1981).

However, all of these attempts should be followed up and more effort and support are needed to make them practical enough for large-scale use. It is evident that in southeast Asia attempts to implement biological control of *Heliothis* spp., either as a single-component system or as a major component in an integrated pest management system, need considerable resources and support before any promising and practical strategies can be evolved.

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Distribution and Economic Importance of *Heliothis* spp. (Lep.: Noctuidae) and Their Natural Enemies and Host Plants in Western Europe

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ABSTRACT

In Western Europe, including Southern Europe to Greece, four Noctuid species belonging to the corn earworm complex are quite common: *Helicoverpa armigera* Hübner, *Heliothis peltigera* Schiffermuller, *Heliothis viriplaca* Hufnagel, and *Heliothis nubigera* Herrich-Schaefer, the last in Spain and Portugal.

H. armigera is the most destructive of them in southern Europe, causing economically significant crop losses on corn, tomato, cotton, tobacco, and many other host plants. A summary of the data on biology, migration, and seasonal occurrence on several crops is presented for *Heliothis* spp. Parasitoids and predators are listed, as well as host plants.

The establishment of a European Workshop on *Heliothis* spp. is mentioned. The concerned research centers are presented, with their main work on the pest and its host plants, and research on parasitoids, rearing techniques, and release.

PROLOGUE

In 1985, a first meeting of the European Workshop on *Heliothis* was held in Cordoba, Spain, to share knowledge on *Heliothis* spp. and to coordinate future efforts to study and control these important noctuids in Europe.

Four laboratories, each with some specialization in *Heliothis* research were involved:

1. The INRA Research Station, Avignon, France. Dr. S. Poitout's team

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has been mainly concerned with noctuid studies for the last 20 years. Light-trap networks have been built up during 9 years and artificial diets have been developed for rearing all species of noctuids. Intensified studies have been conducted on insect development (ecophysiology) and genetics, inbreeding, population dynamics of adults and larvae, and intrapopulation and interpopulation variability.

Recently, pheromone traps have been used very successfully for *H. armigera*.

2. The INIA Research Station at Cordoba, Spain. The team led by Dr. P. Vargas Piqueras is mainly concerned with *Trichogramma* discovery, mass rearing on the alternative host, *Ephestia kühniella,* and first field application of mass-reared egg parasites, with subsequent successful control.

3. The University of Evora, Portugal. The team led by Prof. J. Araujo in Portugal has been concerned for several years with assessing *Heliothis armigera* populations on tomato by collection of eggs, larvae, and adults of this noctuid in the field throughout the cropping season. Egg and larval parasites are noted throughout the season.

4. The USDA European Parasite Laboratory at Behoust, France. The team led by Dr. D. Perkins has been mainly concerned with discovery and rearing of promising parasites of European *Heliothis* spp. for control of *Heliothis zea* in the USA.

The main parasites found by this team, as by all other teams, were *Cotesia kazak* and *Hyposoter didymator.* In addition, a highly virulent strain of the pathogen, *Beauveria bassiana,* was discovered in Spain.

One of the questions treated during the first workshop was the need to work out uniform sampling methods for field collections.

During the first meeting it was decided that members of the work groups should be represented at the *Heliothis* International Symposium that had been proposed for India. This paper is therefore from all members of the European Workshop on *Heliothis.*

INTRODUCTION

In Southern Europe, some representatives of the *Heliothis* complex are of economic importance. Man plays a role by choosing and planting an abundance of crops that serve as preferred food for *Heliothis* larvae. Endemic populations may cause constant loss, and migrating ones may in some years cause even heavier crop loss, especially on corn, tomato, cotton, and tobacco. Migrating pests such as locusts, birds, etc., cause great losses because they leave their natural enemies behind when they migrate. *Heliothis* is no exception. Development of appropriate strategies

to control these pest noctuids in European agriculture requires knowledge of their geographical distribution, migration patterns, and seasonal occurrence and abundance. Several European institutions and laboratories are currently investigating these areas. The host plants, parasitoids, and predators of *Heliothis* in Western Europe are listed. The present review aims to summarize some of the knowledge on *Heliothis* spp. accumulated in Europe during the last decade or so, with emphasis on developments in the laboratories participating in the European Workshop on *Heliothis* (see authors).

HELIOTHIS SPP. AND THEIR GEOGRAPHIC DISTRIBUTION IN EUROPE

Helicoverpa armigera commonly occurs in southern Europe from the Mediterranean shore up to the 45th parallel. There it constitutes a danger to crops but is sporadic. As noted in the CAB Distribution Map (1968) *Heliothis* occurs up to the shore of the Baltic Sea and even Scandinavia. Poitout (1972) states, "This noctuid of sub-tropical origin survives winter conditions with difficulty, overwintering in the pupal stage. It can only continue a normal life cycle if there is contact between endemic and migrating adults" (Poitout 1972). Studies on migration of *H. armigera* and other noctuids are under way for the whole Mediterranean area, with data being collected and evaluated by the team of Dr. Poitout at Avignon, France.

Heliothis (= *Chloridea*) *peltigera* and *H. viriplaca* are present in central and southern Europe. *Nubigera* has only been reported from Portugal (Monteiro 1959) and Spain (Gomez and Arroyo, 1981 cited by Vargas and Cabello, 1985).

The distribution of *Heliothis* spp. also depends on the occurrence of suitable host plants in a susceptible phenological condition during the warm season of the year.

HELIOTHIS SPP. AND THEIR HOST PLANTS

Heliothis spp. are known to be polyphagous, attacking a broad spectrum of crops and wild plants.

H. armigera shows the broadest spectrum of host plants among *Heliothis* spp. in Europe (Table 1). This noctuid feeds preferentially on oil-containing parts of host plants, such as the flower base and seeds (tomato, cotton, corn); however, it may also attack tender leaves and stems (Roome, 1975). There are fewer host plants records for *H. viriplaca* and *H. peltigera* (Tables 2, 3). The host plants of *H. nubigera* are unknown.

Table 1. Host plants of Heliothis armigera *in European countries*

Host plant	Country[1]									
	B	C	F	Ge	Gr	I	P	R	S	Y
Amaranthus sp.			6							
Antirrhinum			2							
Aristolochia sp.			6							
Cabbage			6							
Cannabis sp.				5						
Capsicum sp.	3				2		2		9	
Carnation	2		6, 2		2				9	
Cereals			2							
Chenopodium sp.			6							
Chickpea					2		2			
Chrysanthemum			6				1			
Citrus	2		4			4				
Gladiolus sp.			6		2	2				
Gossypium sp.		2			2			2	2, 9	
Green beans			2				1			
Groundnut	8									
Helianthus sp.			6						9	
Hyoscyamus niger					5					
Lavendula officinalis			6							
Lettuce			6							
Medicago sativa									9	
Nicotiana tabacum	3		7	5	2		8	2	2	
Okra					2					
Pinus radiatus					4	4				
Sesame					2					
Soybean								2		
Sorghum sp.			6						9	
Tomato	3		6	5	2	2		2	2	8
Zea mays	2, 3		2	2	2	2	2		9	2

[1]Country: B=Bulgaria; C=Chypre; F=France; Ge=Germany; Gr=Greece; I=Italy; P=Portugal; R=Rumania; S=Spain; Y=Yugoslavia.

Numbers indicate reference sources: 1. Araujo & Meierrose (1985, pers. comm.); 2. Cortes (1972); 3. Dimitrov (1975); 4. Hardwick (1965); 5. Koch (1958); 6. Poitout & Bues (1979); 7. Quidet (1947); 8. Sidor et al. (1977); 9. Vargas & Cabello (1985, pers. comm.).

Table 2. Host plants of Heliothis viriplaca in Europe

Host plant	Country[1]					
	B	F	Ge	H	I	P
Archotecta calendula						1
Artemisia sp.			2			
Cannabis sp.			2			
Chamaemelum mixtum						1
Cichoria sp.		1	2			
Dipsacus sp.			2			
Gossypium sp.	1					
Herbs		1				
Linum sp.			2			
Lupinus albus						1
Matricaria chamomilla						1
Medicago sativa	1	1		1	1	1
Mentha sp.	1					
Nicotiana tabacum		3				
Ononis repens			2			
Peas					1	
Rumex sp.			2			
Silene implata			2			
Sanchus			2			
Tomato		?				
Zea mays				1		

[1]Country: B = Bulgaria; F = France; Ge = Germany; H = Hungary; I = Italy; P = Portugal. Numbers indicate reference sources: 1. Cortes (1972); 2. Koch (1958); 3. Quidet (1947).

ECONOMIC IMPORTANCE OF *HELIOTHIS* SPP. IN EUROPE

Very little has been done in Europe to estimate crop losses due to *Heliothis* spp. Data from the literature on crop losses are summarized in Table 4. One reason for the lack of estimates is the difficulty in evaluating crop loss due exclusively to *Heliothis* spp. In addition, it is not typical to assess crop losses throughout the season. More often, a one-time-only determination of damage, close to harvest, is used to judge crop loss (Perkins, pers. comm. 1985). Even when crop loss is determined during the whole crop-ping season, it is difficult to translate this loss into economic terms. Loss depends on various factors, such as capacity of the plant to compensate for lost fruits (tomato: Araujo, pers. comm.) or bolls (cotton: Brader, pers. comm.); on market value of the product, which changes throughout the season; on end-product quality required (fungus in tomato concentrate as a secondary effect of *Heliothis* feeding: Araujo & Araujo 1982) or "cosmetic" alterations of corn ears, by producers in Hawaii by cutting off the tops of ears, whether *Heliothis*-attacked or not, for "easier" consumption (Perkins & Mercadier 1984).

Table 3. *Host plants of* Heliothis peltigera *in Europe*

Host plant	Country[1]					
	B	F	G	I	P	S
Archotecta calendula					2	
Atropa belladonna		5	3			
Calendula officinalis		5				
Carthamus tinctorius		5			2, 1	
Chamamaelum mixtum					2	
Chrysanthemum coronarium		5				
Herbacea				4		
Hyoscyamus niger			3			
Inula viscosa		5				
Lavendula sp.		5				
Linaria sp.		5				
Lycopersicum esculentum		5				
Matricaria chamomilla					2	
Mentha sp.	5					
Medicago sativa		5				
Ononis sp.			3			
Salvia pratensis		5	3			
Senecio sp.			3			
Zea mays		5				6

[1]Country: B=Bulgaria; F=France; G=Germany; I=Italy; P=Portugal; S=Spain.
Numbers indicate reference sources: 1. Araujo (1985 pers. comm.); 2. Cortes (1972); 3. Koch (1958); 4. Poitout (1972); 5. Marini & Trentini (1984); 6. Vargas & Cabello, unpub.

Table 4. *Economic importance of* Heliothis armigera *in Europe: percent yield loss*

Country	Crop			
	Corn	Cotton	Tobacco	Tomato
Bulgaria	1930: 10–20%			
France	1951: 10%			
	1962: 14%			
	1982: 15–20%			
	1984: 50%			
Greece		1985: 1–5%	1985: 1–5%	
Portugal				1970: 10–15%
				1973: 25%
Spain		1984: 20%		
Yugoslavia		1985: 1–5%	1985: 1–5%	

Heliothis infestations can be observed each year in the southern area of its distribution, but the intensity of measurable crop loss varies widely from year to year. This might be due to climatic conditions influencing the overwintering endemic generation. Climatic conditions also influence immigration of the noctuids from southern regions.

The presence of *Heliothis* spp. on a crop traditionally leads to heavy pesticide applications, which very often secondarily induce heavy mite attacks. Growers must understand and account for this damage as a secondary effect of *Heliothis*. Costs of pesticides and their application have to be considered part of the economic loss due to *Heliothis* spp. Long-term costs and consequences of pesticides in soil and groundwater pollution are seldom considered, but these "costs" will have to be estimated, too.

HELIOTHIS SPP. AND THEIR SEASONAL OCCURRENCE IN EUROPE

Occurrence of Adult *H. armigera*

France

Since 1984, a network of blacklight Williams-type traps has been progressively built up in southwestern and southeastern France to monitor noctuid occurrence (Poitout 1985). Depending on the regional location of the light trap, catches reveal a continual presence of *H. armigera* adults from mid-May to the end of October (Poitout, pers. comm.). *H. armigera* appeared sporadically by the end of April in Narbonne or mid-May in Perpignan. Poitout and Bues (1979) conclude that there are two generations and a partial third one in southern France.

Portugal

Since 1980, presence of adult *H. armigera* has been monitored throughout the year near tomato fields, using Pennsylvania-type blacklight traps (Meierrose et al. 1985). Activity curves for adult *H. armigera* reveal their presence from the 22nd week (last week of May) to the 45th week (first 10 days of November). Three main peaks can be distinguished, with intervals of about 5 weeks, indicating the occurrence of about three generations. These observations (Fig. 1) were confirmed by egg counts from host plants (Meierrose and Araujo 1984). Similar results were obtained by Guerra and Vintem (1979), who determined the existence of three generations and a partial fourth one.

Spain

Cabello (pers. comm. 1985) confirmed the existence of three generations in Andalusia, with moths starting to appear at the end of May.

Morocco

Hmimina (1980) affirmed the existence of four generations of *Heliothis* and a partial fifth one.

Occurrence of Adult *H. peltigera*

France

In light traps in Istres, France, 107 *C. peltigera* adults were caught from February to October 1964–1969. From traps in Chateau Blanc (Durance), combined captures (76 adults) between 1968 and 1977 showed the occurrence of adults of this species from the last week of March to the end of September. Near Narbonne, combined captures (412) between 1966 and 1972 indicated adult occurrence only from the second week of May to the end of August.

C. peltigera cannot hibernate in France (Poitout 1985), not even in the southeast, and appears annually in spring, brought by air currents moving from south to north. Theoretically, climatic conditions should enable *C. peltigera* to produce three annual generations in southern France.

Portugal

In Portugal, *C. peltigera* is only sporadically caught in light traps, since this species is not normally associated with tomato fields. In 1980, the studied tomato field was bordered by an oil thistle field (*Carthamus tinctorius*), and *C. peltigera* was present during the whole cropping period (Araujo, pers. comm.). In interpreting flight activity curves of *Heliothis* spp., therefore, it is important to consider crops or plants present at the location of the traps.

Occurrence of Adult *H. Viriplaca*

France

Poitout suggests that *C. viriplaca* could reach three annual generations in southern France and overwinter in the pupal stage. Adults are caught from April to September (Istres) and from May to September (Chateau Blanc and Narbonne). Activity curves have been developed from a base of 1076 individuals during the years 1964–69 in Istres, 97 individuals during 1966–72 in Narbonne, and 188 individuals during 1968–77 in Chateau Blanc (Poitout, pers. comm.).

Portugal

C. viriplaca is common and abundant in light traps associated with tomato fields between the 25th and the 40th week (mid-June to the beginning of October) and is likely to present three generations (Araujo, pers. comm.).
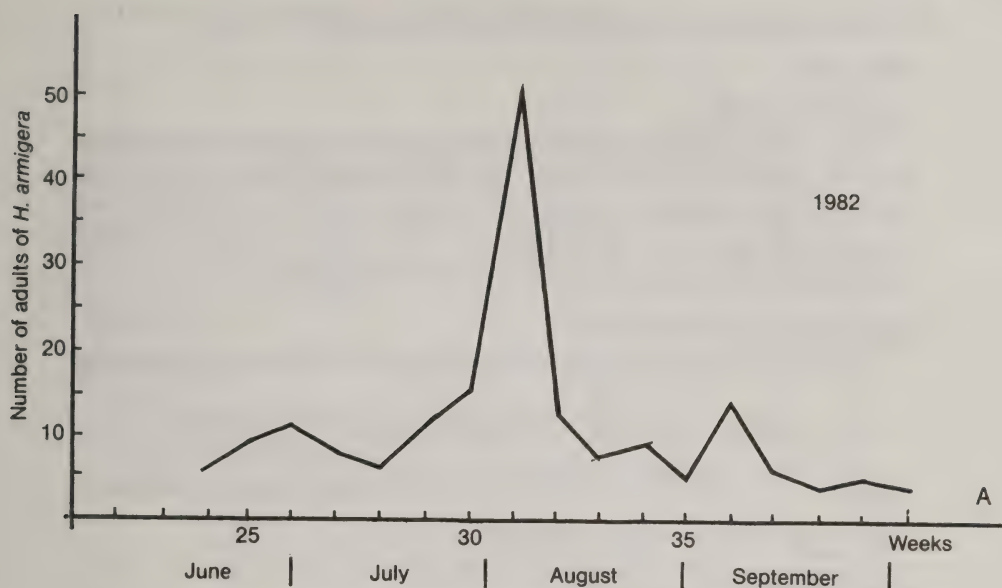
Figure 1. Occurrence of adult *Heliothis armigera* caught daily in a Pennsylvania type blacklight trap near tomato fields in Portugal, 1982.

BIOLOGY OF *HELIOTHIS* SPP.

H. armigera is the best studied of the *Heliothis* spp. in Europe, because of its economic importance. This paper updates findings and presents data that differ from one European country to another, or that are important for biological control activities, and does not repeat general knowledge.

According to Poitout and Bues (1979), adult longevity (from field-collected larvae) in the laboratory under simulated field conditions varies from 5 to 30 days, with an average of 20 days. Fecundity varies (in France) with between 300 and 1800 eggs laid per month and an average of 700 eggs per female. Hardwick (1965) reported an average of 1702 eggs per female *H. armigera* and a maximum of 4394.

H. armigera has five to six larval instars during its development (Poitout and Cayrol 1969). The optimal temperature for continuous development without causing diapause is about 25°C, with 16 hours light and 8 hours dark. At a constant temperature of 15°C, only some individuals are able to develop completely. Under experimental conditions (18–20°C and short-day illumination), many individuals interrupt development for 250 to 300 days. This physiological phenomenon permits part of the population to hibernate in France. Thus, 90% of the instars starting development in mid-August and all starting in mid-September undergo diapause, which in nature is broken during May (Poitout and Bues 1979).

HELIOTHIS SPP. AND THEIR NATURAL ENEMIES IN EUROPE

Parasitoids

Listing parasitoids

Work with field-collected *Heliothis* eggs and larvae will nearly always result in discovery of parasitoids. The list of parasitoids presented here (Tables 5, 6, 7) has been developed from data from literature (without guarantee of systematic precision) and from results of field work by various authors using systematically precise designations.

Quantitative parasitoid data

Quantitative data on parasitoids are difficult to obtain, as the sampling

Table 5. Parasitoids of Heliothis armigera in Europe

ORDER Family Parasitoid	Country	Stage parasitized	Reference[1]
HYMENOPTERA			
Braconidae			
* *Apanteles flavipes* Cam.	UK	Larva	5
Apanteles papilionis Vier.	UK	Larva	5
* *Apanteles ruficrus* Hal.	UK	Larva	5
Bracon brevicornis Wesm.	Europe	Larva	3
Bracon hebetor Say	Turkey	Larva	3
Cotesia kazak Telenga	Europe	Larva	2, 4
* *Microbracon brevicornis* Wesm.	Bulgaria	Larva	5
Ichneumonidae			
Hyposoter didymator	Europe	Larva	2, 3, 4
* *Paniscus ocellaris* Thoms.	Germany	Larva	5
Trichogrammatidae			
Trichogramma cordubensis Varg.	Spain	Egg	7, 8
Trichogramma evanescens	Spain	Egg	6
Trichogramma rhenana Varg.	Portugal	Egg	2
Trichogramma sp.	Portugal & Spain	Egg	6
Selionidae			
Telenomus sp.	Portugal	Egg	1
DIPTERA	Spain	Egg	6
Tachinidae			
Compsilura consinnata Mg.	France	Larva	3
Exorista segregata Rond.	Spain	Larva	3
* *Winthemia quadripustulata* F.	Europe	Larva	5
Unidentified	Europe	Larva	3

[1]Numbers indicate reference sources: 1. Meierrose and Araujo (1984); 2. Meierrose et al. (1985); 3. Perkins and Mercadier (1984); 4. Poitout (pers. comm.); 5. Thompson (1946); 6, 7. Vargas and Cabello (1984, 1985); 8. Vargas and Cabello (pers. comm.).

*Without guarantee of taxonomically authoritative identification.

Table 6. Parasitoids of Heliothis peltigera in Europe

Family Order Parasitoid	Country[1]	Stage parasitized		
		Egg	Larva	Pupa
Hymenoptera, Braconidae				
*Aspilota insidiatrix Marsh.	UK		+	
*Meteorus pulchicornus Wesm.	France		+	
*Orthostigma pumilla Nees	UK		+	
Hymenoptera, Ichneumonidae				
*Hemiteles sp.	France		+	
Diptera, Tachinidae				
*Tachina fera L.	France		+	
*Winthemia quadripustulata F.	France		+	

[1]Reference: Thompson (1946).
*Without guarantee of taxonomically authoritative identification.

Table 7. Parasitoids of Heliothis viriplaca in Britain

Parasitoid	Reference
Hymenoptera, Ichneumonidae	
*Anilastus ruficinctus Grav.	
*Animalon cerinops Grav.	
*Campoplex bucculentus Hlgr.	Thompson (1946)
*Campoplex pugillator L.	
*Schizipyga circulator Panz	
*Tricholobus strigatorius Grav.	

*Without guarantee of taxonomically authoritative identification.

methods are not yet well developed. Depending on the size of the *Heliothis* population, it is possible to collect enough parasite material to verify that significant parasitization exists. The population dynamics of each parasitoid may vary throughout the cropping season, depending on various factors, such as temperature and humidity, daylight duration, etc. If parasitoid counts are made, they are usually made during one moment on one crop at several places. Figure 2 shows the combined seasonal incidence of parasitoids on tomato crops in Portugal, data being collected weekly (Meierrose and Araujo 1984; Meirrose et al. 1985).

Predators

Listing predators

Population control by predators is always somewhat hypothetical. It is not only difficult to evaluate how specific a predator is in the open field, but also how much it may consume per day of a given pest insect. Labora-
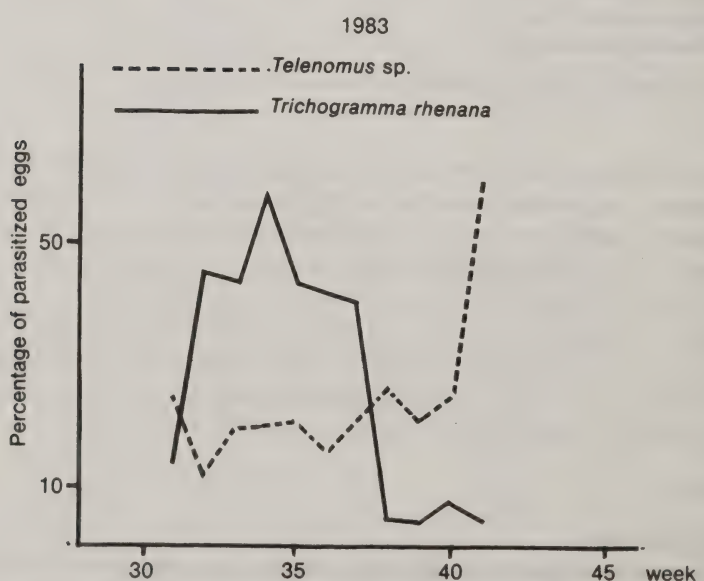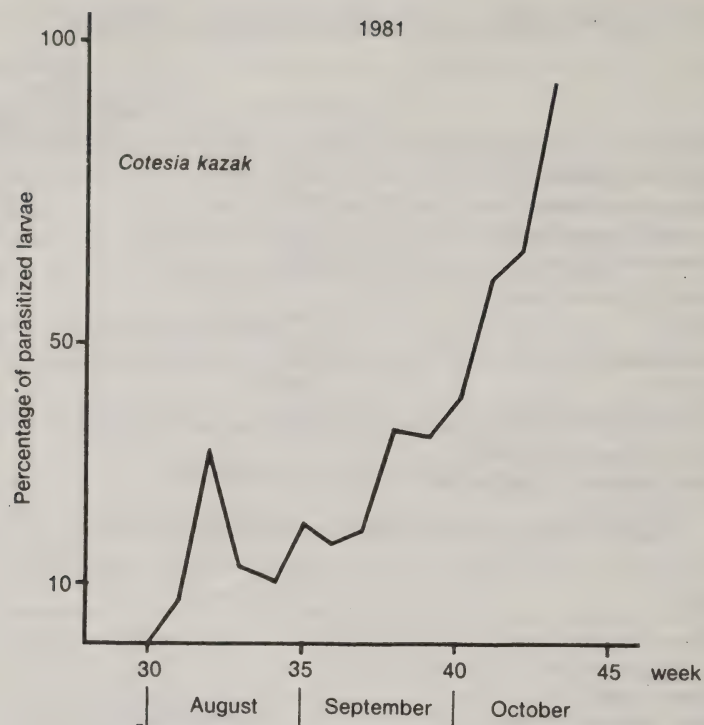
Figure 2. Rates of parasitization by egg and larval parasitoids on *Heliothis armigera* collected from tomato fields in Portugal, 1981.

tory studies cannot give an accurate picture. Nevertheless, we present a list of potential predators, normally encountered by the authors associated with *Heliothis* spp. in crops (Table 8).

Table 8. *Predators and pathogens of* Heliothis *spp. in Europe*

Name	Country	Heliothis stage		
		Egg	Larva	Pupa
Predator				
Ants	Europe (2)	+	+	
Anthocorids (*Orius*)	Europe (2)		+	
Chrysopidal (*C. carnea*)	Europe (2, 1)	+	+	
Coccinellidal (*C. septempunctata*)	Europe (2, 1)	+	+	
Nabids	Europe (2)	+	+	
Pentatomids	Europe (2)		+	
Spiders	Europe (2)		+	
Birds	Europe (1)		+	+
Ardeola ibis	Portugal (1)			+
Pathogen				
Beauveria bassiana	Spain (2)		+	
Nuclear polyhedrosis virus	Yugoslavia, on tobacco (3)			+

[1]Numbers in parentheses indicate reference sources: 1. Araujo and Meierrose (1985, pers. comm.); 2. Perkins & Mercadier (1984); 3. Sidor et al. (1977).

Diseases of *Heliothis* spp. in Europe

Although *Beauveria bassiana* has been known to attack *Heliothis* in nature, it has never been successfully exploited. There is hope, however, of using a very virulent strain of the disease collected in Spain on *Heliothis* larvae (Perkins, 1985, pers. comm.).

In Yugoslavia, *Heliothis* larvae on tobacco were found to be killed by a nuclear polyhedrosis virus (Sidor et al. 1977).

CONCLUSIONS

Of the four species belonging to the corn earworm complex in Europe, *H. armigera* is economically the most important, and it occurs on a large variety of crops. However, although we are aware of the economic importance of *H. armigera,* there is difficulty in evaluating and comparing the attack levels on the various crops.

An impressive number of *Heliothis* enemies have been discovered, identified, and listed, but little is known of nematodes and pathogens.

In the 1980's in Europe, *Heliothis* control using first releases of mass-reared native *Trichogramma* spp. have been attempted, often with good results (Cabello Garcia et al. 1985; Perkins and Mercadier 1984; Araujo and Meierrose, pers. comm. 1985). This leads us to believe that mass-rearing of other parasitoid species may hold promise.

Much work remains to be done in rearing and mass release of larval parasites. Nematodes and pathogens should be sought and tested. A combined attack by many types of biological control agents would present an efficient alternative to traditional pesticidal control of *Heliothis* spp. in Europe.

LITERATURE

In addition to the references cited in the paper, we have included other references (Appendix 1) that may help interested readers find more detailed information on some subjects that could only be treated superficially in this paper. Some references represent work done on *Heliothis* spp. in the laboratories represented at Cordoba, Spain, during the European Workshop on *Heliothis*.

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Distribution and Economic Importance of *Heliothis* and of Their Natural Enemies and Host Plants in Southern and Eastern Africa

D.J. Greathead and *D.J. Girling**

ABSTRACT

Four species of *Heliothis—H. armigera* (Hübner), *H. assulta* (Guenée), *H. fletcheri* (Hardwick), and *H. peltigera* (Schiffermüller)—are of economic importance in Africa. The first two are present throughout the Afrotropical region; *H. fletcheri* is confined to the Sahel, and *H. peltigera* is only recorded once from Ethiopia on safflower. *H. armigera*, which is highly polyphagous, is chiefly known as a pest of cotton and is also an important pest of tobacco, maize, sorghum, millet, pigeonpea and other legumes, vegetables especially tomatoes, sunflower, and citrus. *H. assulta* feeds almost exclusively on Solanaceae and is a pest of tobacco in southeast Asia. *H. fletcheri* has recently been recorded infesting sesame in the Sudan. Recent studies on *H. armigera* are briefly reviewed in relation to information on its biology, ecology, host plants, and economic importance. Revised lists of natural enemies are presented with comments on their potential as biological control agents as an update to the information summarized in ICRISAT (1982).

INTRODUCTION

The literature on economic entomology in Africa contains extensive references to *Heliothis* spp. i.e., the "American bollworm", as a serious pest of a large number of crops, but most detailed studies on their biology and control have been carried out on cotton. Knowledge acquired up to the mid-1950s was reviewed by Pearson (1958). More recent work in Africa was evaluated by the contributors to the International Workshop on *Heliothis* Management (ICRISAT 1982), which includes evaluation of insect natural enemies by Greathead and Girling (1982) and King et al. (1982). The present review is based on these sources and draws attention to current investigations.

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HELIOTHIS SPP. IN AFRICA

Four species of *Heliothis* are reported as of economic importance in Africa. Although other species are known from museum specimens and light-trap catches (e.g. Hardwick 1965; Vermeulen and Catling 1980) nothing is known of their host plants and biology. The four important species are:

> *H. armigera armigera* (Hübner)—found throughout the continent and is of major economic importance;
>
> *H. assulta afra* (Hardwick)—confined to the countries south of the Sahara (Afrotropical region), is believed to feed almost exclusively on Solanaceae, and is a pest of tobacco in southeastern Asia (Hardwick 1965) but is seldom mentioned in the economic literature from Africa;
>
> *H. fletcheri* (Hardwick)—described by Hardwick (1965) from museum specimens caught at localities in the Sahel zone (the most recent of which was captured in 1920) but was not recorded again until 1978 when specimens were reared from sesame and sorghum in the Sudan (Hackett and Gatehouse, 1979);
>
> *H. peltigera* (Schiffermüller)—essentially a Eurasian species, has been reported as causing slight damage to safflower in Ethiopia (Schmutterer, 1971) but has otherwise not been reported as a pest in Africa.

Thus, *H. armigera* is the only species of major economic importance in Africa but because of difficulties in identification, without dissection of the genitalia (Hardwick 1965), other species may have been overlooked by investigators working in the field. Therefore, the published literature is overwhelmingly concerned with *H. armigera*, and the remainder of this review will be confined to discussion of this species.

H. ARMIGERA

Economic Importance

H. armigera is extremely polyphagous and has been recorded on a large number of field and horticultural crops (Table 1). Its importance as a pest relates to its attack on the flowers, buds, and fruit. So it is of greatest significance when the fruit is the harvested product. Being a "direct" pest, economic injury levels are low and control measures become economic at very low population densities.

Most research in Africa on *H. armigera* relates to its importance as a pest of cash crops, especially cotton, rather than food crops. In most instances, estimates of damage have been obtained from pesticide trials and relate to the overall effect of treatments on yield. Since in most

Table 1. Crop hosts of Heliothis armigera *in eastern and southern Africa*

Gymnospermae		
Pinaceae	Pine	*Pinus*
Angiospermae		
Monocotyledones		
Alliaceae	Onion	*Allium*
Graminae	Barley	*Hordeum*
	*Maize	*Zea*
	*Millet	*Eleusine, Pennisetum*
	Oats	*Avena*
	*Sorghum	*Sorghum*
	Wheat	*Triticum*
Dicotyledones		
Caryophyllaceae	Carnation	*Dianthus*
Compositae	*Sunflower	*Helianthus*
Cruciferae	Oil radish	*Raphanis*
Cucurbitaceae	Cucumber	*Cucumis*
	Marrow	*Cucurbita*
	Pumpkin	*Cucurbita*
Geraniaceae	Geranium	*Pelargonium*
Leguminosae	Beans	*Dolichos, Phaseolus*
	*Chickpea	*Cicer*
	*Cowpea	*Vigna*
	*Groundnut	*Arachis*
	Lucerne	*Medicago*
	*Pea	*Pisum*
	*Pigeonpea	*Cajanus*
	Sunnhemp	*Crotalaria*
Linaceae	Flax	*Linum*
Malvaceae	*Cotton	*Gossypium*
	Okra	*Hibiscus*
Moraceae	Hemp	*Cannabis*
Rubiaceae	Coffee	*Coffea*
Rutaceae	Citrus	*Citrus*
Solanaceae	Cape gooseberry	*Physalis*
	Eggplant	*Solanum*
	*Pepper	*Capsicum*
	*Tobacco	*Nicotiana*
	*Tomato	*Lycopersicon*
Umbelliferae	Carrot	*Daucus*

*Crops on which serious infestations are reported.

instances there was a complex of pests attacking the crop, it is not possible to isolate loss due to *H. armigera.* For example, cotton is damaged by a wide range of pests, including several genera of bollworms; similarly, there is usually a complex of pod borers affecting pulses. The situation is less confused in some other crops, e.g. tomatoes, where other pests are not

causing similar damage. Damage to cereals is usually less important, since the major losses are caused by stem borers, and in maize *H. armigera* usually only affects the silks and the unproductive apices of the cobs. Economic importance is also greatly influenced by the cropping sequence and the presence of other susceptible plants.

By relating numbers of *H. armigera* eggs on cotton in Malawi to subsequent loss of yield, Matthews and Tunstall (1968) obtained data showing losses ranging from 112 kg seed cotton/ha with 0.25 egg per plant to 820 kg with 1 egg per plant. They concluded that control is necessary when the egg count reaches 0.5 per plant. Recent work in South Africa (van Hamburg 1981; pers. comm.) has questioned this conclusion because of inconsistent results related to variability in the viability of eggs (between 50% and 80% viable), and therefore a threshold for control of 2 larvae per 12 plants has been proposed. Using this index, fewer sprays are required, cutting costs of control by 60%.

Host Plants

H. armigera has been recorded as a pest of at least 36 crops in eastern and southern Africa (Table 1) and many genera of wild host plants (Table 2). This list is not complete and with such a polyphagous species it is unlikely that a comprehensive listing is possible. The crops include both monocotyledons and dicotyledons and even a gymnosperm (*Pinus*); however, all the records of wild hosts we have located are dicotyledons. Most of these records have been gathered during studies on the dynamics of *H. armigera* in crops (e.g. Parsons 1939). They therefore, relate to weeds that are abundant on arable land and so constitute sources for infestation of the crop. Monocotyledons in these situations (grasses and sedges) do not have large nutritious inflorescences that would attract *H. armigera*, which would account for their absence from the records.

There is great variability in the suitability of the various host plants for development. Laboratory studies by Pretorius (1976) measuring survival, rate of development, and fecundity of the progeny reared on 12 different food plants concluded that overall the highest net reproductive rate was achieved on cotton flower buds but that maize cobs ranked low. His results contrast with the frequent conclusion of field observations (e.g. Pearson 1958) that cotton is not a most favored host plant and that attack on cotton is associated with the presence of other hosts in the neighborhood and their phenology. Thus, in the Sudan Gezira, *H. armigera* has assumed the status of a major pest on cotton only since groundnuts have been grown in the rotation. The groundnuts provide an out-of-season host (e.g. Proctor, 1974). An interesting study by Rens (1977) on *H. armigera* infestations in smallholder agriculture in Kenya provides another example. He found

Table 2. Heliothis armigera: *wild host plants in eastern and southern Africa*

Angiospermae	
Dicotyledones	
Acanthaceae	*Justicia*
Amaranthaceae	*Amaranthus*
Capparidaceae	*Cleome*
Chenopodiaceae	*Chenopodium*
Compositae	*Bidens*
	Sonchus
	Tagetes
	Tridax
	Xanthium
Convolvulaceae	*Ipomoea*
Euphorbiaceae	*Acalypha*
Labiatae	*Hoslundia*
	Leucas
	Ocimum
	Orthosiphon
Malvaceae	*Abutilon*
	Malvastrum
	Sida
Papaveraceae	*Papaver*
Portulacaceae	*Portulaca*
Scrophulariaceae	*Striga*
Solanaceae	*Datura*
	Nicandra
	Physalis
	Solanum

*Weed species reported as important alternative hosts.

that it infests maize in preference to cotton, so that damage to cotton was directly related to the distance from the nearest maize, and that interplanting with beans intensified attack on cotton. In northern Tanzania, Nyambo (1984) has shown that the weed *Cleome* sp. and a sequence of crops—maize and sorghum followed by cotton—maintain a high level of infestation throughout the growing season.

Natural Enemies

Parasitoids

The numerous species of insect parasitoids of *H. armigera* reported from southern and eastern Africa are listed in Table 3, with a reference to their first mention in the literature. Usually there is no indication of the importance of the parasitoid as a natural mortality factor. Where authors have indicated that a species is important or provide evidence that it

Table 3. *Parasitoids of Heliothis armigera in eastern and southern Africa*

Parasitoid	Host Plant	Country	Reference	Importance
Braconidae				
Aleiodes sp. nr. *pallidator* (Thnb.)	Cotton	Uganda	—	—
Apanteles maculitarsis Cam.	Various	S. Africa	Parsons 1940a	Important
Apanteles sp. nr. *aethiopicus* Wlkn.	Peas	S. Africa	Parsons 1940a	Important
Apanteles sp. *ultor* group	Cotton	Uganda	Coaker 1959	Up to 20%
Apanteles sp.	—	Somalia	Russo 1940	—
Ascogaster ?cava Saeger	Cotton	Uganda	Coaker 1959	Rare
Bracon brevicornis Wesm.	Various	S. Africa	Parsons 1940a	V. common
Bracon sp.	Cotton	Tanzania	Le Pelley 1959	—
Braunsia sp.	Cotton	Tanzania	Le Pelley 1959	—
Cardiochiles nigricollis (Cam.)	Various	S. Africa	Parsons 1940a	Common
C.?nigromaculata (Cam.)	Cotton	Tanzania	Reed 1965	—
C. trimaculata (Cam.)	Cotton	Uganda	Coaker 1959	V. important
Chelonus bifoveolatus Szepl.	Cotton	Tanzania	—	—
C. curvimaculatus (Cam.)	Cotton	Uganda	Coaker 1959	Rare
C. curvimaculatus Cam.	Maize	S. Africa	Parsons 1940a	Common
C. curvimaculatus Cam.	Citrus	S. Africa	Prinsloo 1984	—
C. pilosulus Szepl.	Cotton, beans	Sudan	Lazarevic 1971	—
C. versatilis (Wlkn.)	Cotton	Sudan	Wilkinson 1932	—
Chelonus sp.	Cotton	S. Africa	Simmonds 1960	—
Chelonus sp.	Citrus	Zimbabwe	Hall & Ford 1933	Rare
Disophrys sp.	Cotton, beans	Sudan	Lazarevic 1971	—
Meteorus laphygmarum Brues	Cotton	Uganda	Coaker 1959	—
Meteorus laphygmarum Brues		Sudan	Nixon 1943	Rare
Meterous sp.	Cotton	Tanzania	Reed 1965	Rare
Ichneumonidae				
Charops sp.	Legumes	Tanzania	Reed 1965	Common

Species	Crop	Country	Reference	Percentage
Charops sp.	Cotton	Uganda	Coaker 1959	Up to 10%
Charops sp.	Cotton, tomato	S. Africa	Parsons 1940a	V. rare
Diadegma sp.	Peas, maize	S. Africa	Parsons 1940a	Rare
Enicospilus sp. nr. *communis* Szepl.	Cotton	Uganda	Coaker 1959	Up to 10%
Metopius discolor Tosq.	Cotton	Tanzania	Reed 1965	—
	Various	S. Africa	Parsons 1940a	—
Netelia ?capensis Hlmgr.	Cotton	Uganda	Coaker 1959	Rare
N. opaculus (Thoms.)	—	Kenya	Le Pelley 1959	—
Netelia sp.	Cotton	Tanzania	Reed 1965	Up to 3%
Pristomerus sp. nr. *fumipennis* (Wlkn.)	Cotton	Uganda	Coaker 1959	Rare
Pristomerus sp.	Cotton	Tanzania	Reed 1965	—
Pristomerus sp.	Various	S. Africa	Parsons 1940a	Rare
Chalcididae				
Brachymeria bottegi Masi	Tobacco	Zimbabwe	Bünzli & Buttiker 1957	Rare
B. cowani Kirby	Cotton	Tanzania	Reed 1965	—
Brachymeria sp.	Cotton	Uganda	Coaker 1959	—
Eulophidae				
Euplectrus sp.	Peas	S. Africa	Parsons 1940a	—
Trichogrammatidae				
Trichogrammatoidea lutea Gir.	Cotton	S. Africa	Parsons 1940a	up to 60%
Trichogrammatoidea lutea Gir.	Maize	Zambia	Bebbington & Allan 1935	Important
	Citrus	Zimbabwe	Jones 1937	—
	Citrus	S. Africa	Prinsloo 1984	—
Trichogrammatoidea sp.	Cotton	Tanzania	Reed 1965	up to 5%
Trichogrammatoidea sp.	Cotton	Uganda	Coaker 1959	—
Trichogrammatoidea sp.	—	S. Africa	Jones 1937	—
Scelionidae				
Platytelenomus busseolae (Gah.)	Cotton	Uganda	Coaker 1959	—
Platytelenomus busseolae (Gah.)	Cotton	S. Africa	Parsons 1940a	up to 70%

(continued)

Table 3 continued

Parasitoid	Host Plant	Country	Reference	Importance
Telenomus ullyetti Nixon	Citrus	Zimbabwe	Jones 1937	—
Telenomus sp.	Cotton	S. Africa	Pearson 1958	Important
Telenomus sp.	Citrus	Zimbabwe	Hall & Ford 1933	—
	Winter crops	S. Africa	Parsons & Ullyett 1934	Up to 50%
Bombyliidae				
sp. indet	Maize	S. Africa	Parsons & Ullyett 1934	Up to 27%
	Cotton	S. Africa	Pearson 1958	—
Calliphoridae				
Amobia signatus (Mg.)	Citrus	Zimbabwe	Hall & Ford 1933	—
Sarcophaga sp.	Cotton	Tanzania	—	—
	Maize	Somalia	Chiaromonte 1933	—
Tachinidae				
Carcelia ?evolans (Wied.)	Cotton	Tanzania	Reed 1965	Rare
C. illota (Curr.)	Cotton	Tanzania	Robertson 1973	Up to 40%
C. illota (Curr.)	Citrus	Zimbabwe	Hall & Ford 1933	—
Ceromyia cibdela (Villen.)	Cotton	S. Africa	Cuthbertson & Munro 1941	—
Dejeania bombylans (F.)	Cotton	Zimbabwe	Cuthbertson 1934	Abundant
Dejeania bombylans (F.)	Cotton	Tanzania	—	—
Drino partitor (Curr.)	Cotton	Zimbabwe	Cuthbertson 1939	—
Exorista sorbillans (Wied.)	Cotton	S. Africa	Cuthbertson & Munro 1941	—
Exorista xanthaspis (Wied.)	Cotton, beans	Sudan	Lazarevic 1971	—
Gonia bimaculata Wied.	Cotton	S. Africa	Parsons 1940a	Rare
Gonia bimaculata Wied.	Maize	Somalia	Chiaromonte 1933	—
Gonia sp.	Citrus	Zimbabwe	Hall & Ford 1933	V. important up to 12%
Goniophthalmus halli Mesnil	Cotton	Tanzania	Reed 1965	—
		Zimbabwe	Mesnil 1956	—
Linnaemya affinis Corti	Cotton	S. Africa	Taylor 1932	—
L. agilis Curr.	Cotton	Tanzania	Curran 1934	—
L. agilis Curr.	Cotton	S. Africa	Curran 1934	—

Species	Crop	Country	Reference	Status
L. longirostris (Macq.)	Cotton	Uganda	Coaker 1959	—
L. longirostris (Macq.)	Cotton	Uganda	Coaker 1959	—
L. longirostris (Macq.)	Cotton	Kenya	Le Pelley 1959	—
L. longirostris (Macq.)	Cotton	Tanzania	Robertson 1973	Rare
L. longirostris (Macq.)	Cotton	S. Africa	Cuthbertson & Munro 1941	Important
Linnaemya sp.	Tobacco	Zimbabwe	Bünzli & Buttiker 1957	—
Nemoraea capensis (R.D.)	Peas, citrus	S. Africa	Parsons 1940a	Rare
N. rubellana Villen.	Maize	Kenya	Rens 1977	—
Pales blepharipus (Brauer & Berg)	Cotton	S. Africa	Cuthbertson & Munro 1941	—
Pales blepharipus (Brauer & Berg)	Cotton	Zimbabwe	Cuthbertson & Munro 1941	—
P. coerulea (Jeannicke)	Various	S. Africa	Parsons 1940a	—
P. nigronitens Villen.	Cotton	S. Africa	Parsons 1940a	—
P. seminitida Villen.	Cotton	Zimbabwe	Cuthbertson & Munro 1941	—
Palexorista imberbis (Wied.)	Cotton	Tanzania	Reed 1965	Up to 25%
Palexorista imberbis (Wied.)	Cotton	Uganda	—	Rare
Palexorista imberbis (Wied.)	Cotton	Sudan	Pearson 1958	V. important
Palexorista imberbis (Wied.)	Cotton	S. Africa	Parsons 1940a	Important
Palexorista imberbis (Wied.)	Cotton	Zimbabwe	Searle 1964	—
Palexorista imberbis (Wied.)	Maize	Somalia	Chiaromonte 1933	—
Palexorista imberbis (Wied.)	Beans	Sudan	Lazarevic 1971	Important
P. laxa (Curr.)	Cotton	S. Africa	Cuthbertson & Munro 1941	—
Palexorista sp. nr. *inconspicua* (Mg.)	Maize	Somalia	Chiaromonte 1933	—
Palexorista sp. nr. *inconspicua* (Mg.)	Citrus	Zimbabwe	Jones 1939	Important
Palexorista sp. nr. *inconspicua* (Mg.)	Cotton	S. Africa	Parsons 1940a	—
Paradrino halli (Curr.)	Cotton	Tanzania	Robertson 1973	Up to 25%
Paradrino halli (Curr.)	Citrus	Zimbabwe	Jones 1939	—
Paratachina obliqua (Lw.)	Cotton	S. Africa	Cuthbertson & Munro 1941	Rare
Pseudogonia rufifrons (Wied.)	Various	S. Africa	Parsons 1940a	—
Pseudogonia rufifrons (Wied.)	Cotton, beans	Sudan	Lazarevic 1971	—

(continued)

Table 3 continued

Parasitoid	Host Plant	Country	Reference	Importance
Sturmia convergens (Wied.)	*Striga*	Tanzania	—	—
Sturmia sp.	Citrus	Zimbabwe	Hall & Ford 1933	V. important
Thelairosoma angustifrons (Villen.)	Cotton	Zimbabwe	Pearson 1958	—
Voria capensis Villen.	Cotton	S. Africa	Cuthbertson & Munro 1941	—
Winthemia dasyops (Wied.)	Cotton	S. Africa	Cuthbertson & Munro 1941	—
Zygobothria ciliata (Wulp)	Citrus	Zimbabwe	Jones 1939	Rare

achieves a significant level of parasitism, an indication is included in the table. Thus, the number of species recorded as regularly attacking *H. armigera* is only a small proportion of the total. These were discussed by Greathead and Girling (1982), who noted the conclusions of the principal investigations that:

1. high egg-parasitism had little effect on the size of the larval population, and overall mortality was highest on cotton in South Africa (Parsons 1940a);

2. in an area of Uganda where rainfall is relatively uniform throughout the year, overall levels of parasitism were low but so was host density (Coaker 1959);

3. following the dry season in northern Tanzania, parasitism rates were low but built up during the growing season too late to prevent serious damage to cotton and reached a peak at the end of the season on pigeonpea (Reed 1965).

Recent work on cotton in South Africa (van Hamburg 1980; pers. comm.) has detected mean seasonal rates of egg parasitism varying between 5.9% and 34.8% at two sites over 4 years due to *Telenomus ullyetti* and *Trichogrammatoidea lutea*. On most occasions mean parasitism by the former tends to exceed that by *T. lutea*. Total mean parasitism of larvae is currently very low (0.5% in 1984–85), possibly a result of intensive pesticide usage. For example, in Tanzania the mean level of larval parasitism fell from 27% in 1962 to 6.4% in 1964, following the initiation of intensive pesticide application (Reed 1965).

Several authors (e.g. Reed 1965; Nyambo 1984) have drawn attention to higher levels of insect parasitism and greater intensity of disease caused by NPV on maize and weeds than in cotton.

Predators

Until recently, little attention has been paid to the role of predators, largely because of the difficulty in making quantitative observations: thus most records are anecdotal. The species mentioned are listed in Table 4. Pearson (1958) notes that on cotton in South Africa an anthocorid, *Orius insidiosus* (Say) destroys up to 40% of the eggs, *Chrysopa* sp. preys on young larvae, and ants, especially *Pheidole* sp., are most useful in destroying pupating larvae and pupae. Other authors (e.g. Reed 1965) mention pentatomids and wasps as well as anthocorids, chrysopids, and ants. Brettell and Burgess (1973) assessed insecticide toxicity to common field predators, and Brettell (1979) studied the biology and toxicity of pesticides to *C. boninensis* Okomoto in preparation for the introduction of biologically selective pesticidal control for cotton pests in Zimbabwe (Gledhill 1982).

Current work in South Africa has demonstrated that conservation of

Table 4. Predators of Heliothis armigera *on cotton in eastern and southern Africa*

Predator	Country	Reference
Hemiptera		
Anthocoridae		
Orius insidiosus (Say)	S. Africa	Pearson 1958
Pentatomidae		
Glypsus conspicuus Westwood	S. Africa	Taylor 1932
	Tanzania	Reed 1965
Macroraphis acuta Dallas	Tanzania	Reed 1965
Reduviidae		
Coranus papillosus Thunberg	S. Africa	Taylor 1932
Rhinocoris albopunctatus Stål	S. Africa	Taylor 1932
R. segmentarius Germar	S. Africa	Taylor 1932
Neuroptera		
Chrysopidae		
Chrysopa boninensis Okomoto	Zimbabwe	Brettell 1979
Chrysopa sp.	S. Africa	Pearson 1958
	Tanzania	Reed 1965
Chrysoperla congrua Walker	Zimbabwe	Brettell 1979
C. pudica Navas	Zimbabwe	Brettell 1979
Hymenoptera		
Formicidae		
Dorylus sp.	S. Africa	van Hamburg pers. comm.
Myrmica sp.	Tanzania	Reed 1965
Pheidole sp.	S. Africa	Pearson 1958
	Tanzania	Reed 1965
Eumenidae		
Eumenes maxillosus Degeer	S. Africa	Taylor 1932
Sphecidae		
Ammophila sp.	Tanzania	Reed 1965

predators can reduce dramatically the number of applications of cypermethrin required on the cotton crop. Ants have been recorded causing 89% mortality, with a *Dorylus* sp. accounting for 94% of the total (van Hamburg, pers. comm.).

Diseases

McKinley (1982) listed viruses isolated from *Heliothis* spp. and reviewed efforts to apply them as control measures. Little of this work was done in Africa, and most references to the incidence of polyhedrosis viruses in *H. armigera* in the field are anecdotal and refer to the greater incidence of mortality from virus attack on maize rather than cotton (Reed 1965; Rens 1977; Nyambo 1984). Coaker (1959) reviewed work on nuclear polyhedrosis virus (NPV) in South Africa during 1933–34 and described its presence at enzootic levels in larvae on maize and cotton in Uganda.

Biological Control

Application of insect parasitoids as biological control agents was attemptted in South Africa during the 1930s when "*Trichogramma luteum*" was mass-bred and released in cotton fields but the method was not successful (Summarized in Pearson 1958). Further work on *Trichogramma* spp. has been carried out recently, using imported cultures. One species, *T. pretiosum*, was established in the field (van Hamburg 1981); however, attention has now turned to introducing *Apanteles kazak* which is now in culture prior to release (van Hamburg, pers. comm.).

Preliminary trials have been carried out using *Bacillus thuringiensis* and NPV preparations as biological pesticides in Uganda (Coaker 1959), Tanzania (McKinley 1971), and Botswana (Roome 1975) but this work has not been followed up.

DISCUSSION

H. armigera is native in Africa and has a large array of natural enemies, but it is still a major pest. It is highly polyphagous, moving between crops and weeds as they flower and become susceptible to attack, and it is capable of migrating long distances. For these reasons, it does not seem to be a promising target for "classical" biological control; therefore, most recent research has been directed at reducing pesticide usage by developing scouting methods to enable the timing of sprays and minimize interference with native natural enemies. The next step, augmenting these with introduced species, is being attempted in South Africa. However, there are few obvious opportunities since all important parasitoid genera are already present in Africa, but there is the possibility that more effective species may be found which might displace less efficient native species.

Experiments and observations on the interactions between *H. armigera*, its host plants, and levels of mortality, have suggested measures to enhance natural mortality by altering cultural practices. The possibilities are especially attractive on small farms employing traditional methods, where mixed cropping could be adjusted to maximize natural enemy mortality and minimize population buildup.

Possibilities of using microbial agents in place of chemicals have not been pursued because of high cost, short shelf life, and difficulties in finding suitable formulations. Until these problems are overcome, microbial pesticides are not attractive.

It is concluded that the best prospects for biological control in Africa lie in improving understanding of the biology of natural enemies so that cultural controls employed in traditional farming can be improved and other measures can be developed to conserve natural enemies and enhance their impact.

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Exploration, Importation, and Establishment of New Effective Natural Enemies of *Heliothis*

Introduction

R.C. Hedlund*

Many factors affect the success of biological control attempts, not the least of which is the availability of an effective natural enemy. When a pest insect is a recent import into the area where it is causing a problem, the approach to finding natural enemies is fairly straightforward. One simply goes to the region from which the pest came, determines its natural enemies, and selects the most effective ones for establishment attempts in the new location. However, when a pest has been endemic to a region for a long time and new natural enemies must be sought in different regions and from different (albeit closely related) hosts, the difficulties of successful biological control are greatly compounded. This section deals with the problems involved in locating, evaluating, transporting, and establishing natural enemies of *Heliothis* species.

First to be discussed are the attributes of effective natural enemies and the importance of differentiating between effective natural enemies and opportunistic or occasional natural enemies. This paper will make clear the need for adequate ecological and biological studies of potential parasites. The remaining four papers will discuss the importation and establishment of new natural enemies of *Heliothis* into Australia, India, the USA, and New Zealand.

Australia has *Heliothis* spp. as pests over wide-ranging climatic areas and many natural enemy niches are already filled. The introduction of four new parasites appears promising, and the attempts to establish these should yield valuable biological and ecological data.

Numerous parasites of *Heliothis* are present in India and there have been many attempts (some successful) to establish new species. Based on recent importation experience, researchers are able to make some recommendations on what host stages are most susceptible to additional natural enemy attack and from what geographical areas new parasites should be sought.

A thorough review of *Heliothis* natural enemy establishment in the USA is presented and the problems of importation, rearing, and release are discussed. Five parasites are currently being evaluated for release against

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Heliothis in the USA and plans to evaluate the effectiveness of new establishments are presented.

New Zealand has only one established species of *Heliothis* and one parasite, *C. kazak*, has been imported and established. Studies comparing *Heliothis* populations in the absence of *C. kazak* with those attacked by the parasite show clearly the effects of this imported natural enemy.

We hope that subsequent discussion of these presentations will assist researchers in developing general concepts governing exploration for, and importation and release of, natural enemies of *Heliothis*. Increased cooperation among scientists from various countries should promote successful biological control of *Heliothis*.

Attributes of Effective Natural Enemies, Including Identification of Natural Enemies for Introduction Purposes

*K.P. Carl**

ABSTRACT

Classical biological control has difficulties in getting rid of the image of being an art rather than a science, mainly because the outcome of a project remains unpredictable, as many introduction projects of natural enemies have been terminated prematurely. "Old" projects are being taken up again to analyze the reasons for failure. General aspects such as ecological and climatic match; super-, clepto- and multi-parasitism; and multiple introductions are briefly discussed, followed by a remarkable case history which elucidates several important points. Alien parasites can be more effective than specialized native ones, and the founder principle and genetic drift appear to be important genetic components in successful parasite introductions. Attempts to make the outcome of biocontrol programs more predictable by modeling have so far not brought the desired results, but may eventually, through a closer cooperation between mathematicians and ecologists, enabling the collection and analysis of more data. A summary is given of the natural enemies of *Heliothis armigera* recorded during surveys in the Mediterranean. One of these, *Apanteles kazak*, has been established in New Zealand, where it has become an effective control agent of *H. armigera* on soybean.

Although several control methods employing living organisms are now in use, including conservation, inoculation, augmentation, and inundation mostly of native natural enemies, the introduction of exotic species for permanent establishment and control of a pest, often referred to as classical biological control, is still the first choice. "It produces long-term results and is preferred as no further input is required, biological or chemical, once control has been established. With the other methods, regular farmer cooperation is necessary" (Greathead and Waage 1983).

Historically, classical biological control concentrated on the search for effective natural enemies in the native area of introduced pests, on the

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assumption that the target species had left its natural enemies behind and thus escaped natural control. Emphasis has been on the introduction of parasites rather than predators, which are generally less specific and often have equally effective counterparts in the new area, with notable exceptions such as *Rodolia cardinalis* (Mulsant). The success rate with both categories of natural enemies has been similar (Hall and Ehler 1979).

From many examples we now know that native pests are also amenable to biological control by introduced parasites. A statistical analysis of 286 cases of successful biological control by introduction led Hokkanen and Pimentel (1984) to conclude that "new host-parasite associations" have a much higher chance of success than old associations. Although there is neither full agreement about theory nor about the relative likelihood of success, most authors agree on the feasibility of successfully using new host-parasite associations (for a summary see Carl 1982). The widespread neglect of this possibility deprives us of a much larger array of potentially useful natural enemies than we use at present.

According to Clausen (1978), about 30% of parasites and predators introduced against insect pests became established, and about 20% contributed significantly to pest control. This is a seemingly low success rate, although the cost-benefit ratio has been very very positive. A large number of projects has been terminated prematurely due to financial constraints. Beirne (1985) rightly suggested that "every project should be regarded as viable and unfinished until either it is successful or valid reasons why it cannot be are identified."

The following example is a good documentation of this dilemma. The carrot rust fly *Psila rosae* F., of European origin, became a serious pest in Canada. Two principal parasites known from Europe, the braconid *Dacnusa gracilis* Nees and the diapriid *Loxotropa tritoma* Thoms., a larval and a pupal parasite, were studied in detail, released in Canada as large colonies (*Dacnusa*) and in adequate numbers (over 140,000 *Loxotropa*), but neither of them became established. It was stated by McLeod et al. (1962) about *Dacnusa* that "all known conditions were favorable," and about *Loxotropa* that "conditions were favorable" and "through cage releases it was determined that *L. tritoma* parasitized the host pupae and survived the winter in the Holland Marsh area of Ontario. No known reason why this species did not become established in Canada can be suggested."

Fortunately, this project will be taken up again, but had it not been stopped prematurely, like many others, we would undoubtedly be in a better position to evaluate the attributes of potentially effective natural enemies and their response to new environmental conditions. With the present state of affairs one might be tempted to concur with Bennett (1974) that "there are basically only two major considerations when selecting

control agents: (a) that the natural enemy should appear to have the potential to at least partially control the target host species; and (b) that the introduced organism will not cause detrimental effects to the ecosystem." Is there any possibility to add to these very obvious statements?

SOME GENERAL ASPECTS

Some desirable attributes of effective natural enemies are well known (e.g. DeBach 1964). There must be a climatic and ecological match for species to be introduced into a new area. In order to make the best use of their offspring, parasites should have a high reproductive potential, they should avoid super- and multi-parasitism, and they should have a short developmental period and yet be synchronized with the target host.

Much has been said about the relative merits of monophagous versus polyphagous parasites, the latter perhaps being "distracted" from the target host. Obviously, alien natural enemies introduced against native pests cannot be strictly monophagous as otherwise they would not attack the target host.

Hyperparasites should be excluded as control agents. Even recently *Brachymeria secundaria* Ruschka was listed as a primary parasite of *Heliothis armigera* Hb., suggesting that great care must be taken to make the status of a parasite absolutely clear prior to introduction. Only extremists believe these days in the beneficial effects of hyperparasites.

Even more intricate is the role of cleptoparasites which are intrinsically superior competitors that, because of their low searching efficiency, usually follow the odor trail of another primary parasite to find a host and thus suppress extrinsically superior parasites, dipping the balance in favor of the host. Fortunately cleptoparasitism is rare, but its deleterious effect on overall parasitism has been shown by Schroeder (1974) in a study of the parasite complex of the pine shoot moth (*Rhyacionia buoliana* Schiff.).

The question of single versus multiple introductions of natural enemies is still under discussion. It is postulated here that there can be no general "either-or" answer to this question. Usually there have been multiple introductions against a pest; on average seven natural enemies were introduced for each target pest (Hokkanen & Pimentel 1984). If more than one species became established and there was success, it was no longer possible to decide whether the combination was necessary or whether a single species would have produced the same result. A good case is the control of the winter moth in Canada (see below), where two parasites became established and achieved control, but it is still doubtful whether one or both species were necessary.

Multiple introductions may be unnecessary but cannot be harmful

even if competition occurs between parasite species. At worst the intrinsically inferior species will be displaced by competition, otherwise there will be an additive effect. Species belonging to different guilds which do not interfere with each other, will always exert an additive effect.

Searching Efficiency

As Waage and Hassell (1982) stated, the term "searching efficiency" has been "widely used in the biological control literature, but rarely with a precise definition in mind." That the term is ambiguous is obvious. Clearly, to the biological control worker, a species with high searching efficiency is one that is common in low host populations, but this information is of little help to the modeler. Presumably, the natural enemies with high fecundity and high searching efficiency are the most likely to bring about control, unaided by other species.

A classical example is the winter moth—*Cyzenis albicans* Fall.—*Agrypon flaveolatum* Grav. system in Canada. Both parasites were introduced from Europe against the pest of European origin, and control ensued (Embree 1971). It was postulated that *Cyzenis* with high fecundity but low searching ability reduced the high population levels of the host and that *Agrypon* with low fecundity but high searching efficiency kept it at this level. A model developed by Hassell (1980) casts doubt on the usefulness of *Agrypon*, but the question remains unresolved, as the experiment is irreversible.

Reproductive Potential

A high reproductive rate of a natural enemy is desirable, but this criterion often seems to have been misinterpreted. It would certainly be misleading to compare different taxa with vastly different reproductive rates, e.g., some ichnemonids or braconids with a potential reproductive rate of less than 100 per female, with tachinids producing several thousands of microtype eggs, or certain polyembryonic encyrtids (e.g. *Ageniaspis, Copidosoma, Litomastix*) producing up to several thousand offspring from one egg. A high reproductive rate must be counteracted by other factors.

For instance, one of the parasites attacking *H. armigera* in Egypt is *Copidosoma* sp., which produces up to 615 adults from a single host larva. On the face of it, this polyembryonic species ought to be the most important parasite in the area—but it is not. One of the compensating factors may be that there is only one generation per year, while the host reproduces four times (El-Heneidy and Abbas 1983).

Another example is tachinids with microtype eggs produced by the thousands that might be considered as good biocontrol agents, but their precarious mode of reproduction (the eggs are laid on the host food

substrate and have to be eaten) could be a hindrance. *C. albicans* is a representative of this group. Embree's (1971) work suggests that *Cyzenis* achieved control of high winter moth populations in which it could become effective because a high proportion of its eggs were eaten by the host, but other tachinids with microtype eggs are known that fail to reduce high populations of their hosts substantially.

Even in comparing closely related species, great caution is warranted. We compared the solitary *Apanteles kazak* Telenga with the gregarious *Apanteles* sp. (*glomeratus* group) in relation to *H. armigera*. Both may now be assigned to different genera but are sufficiently close to draw a comparison which should be in favor of the gregarious species. Laboratory studies confirmed that *Apanteles* sp. was about 3.5 times as fecund as *A. kazak*, but in the field it is virtually nonexistent (ratio to *A. kazak* about 1 : 6500). The reasons are obscure; for instance, the gregarious species may have another principal host which remains unknown as long as the parasite cannot be identified to the specific level. However it should be noted that there are several gregarious *Apanteles* species of the *glomeratus* group that are likewise ineffective.

These few examples show the difficulties of using fecundity as a yard-stick of parasite performance. On the face of it, *A. kazak* or *Hyposoter didymator* Thunb. producing less than 100 offspring would appear unlikely to control *H. armigera* which produces close to 1000 progeny, but other parasites in similar situations have.

A REMARKABLE CASE HISTORY

The following case history may serve to introduce some further subjects. For many years, attempts were made in Barbados to establish several tachinids against the neotropical sugarcane borer, *Diatraea saccharalis* F., without tangible success, although some of the species, particularly *Lixophaga diatraeae* Tns., *Paratheresia claripalpis* Wulp, and *Metagonistylum minense* Tns. had been successful elsewhere in the Caribbean (Simmonds 1959). Only *L. diatraeae* eventually became established with great difficulty, after several strains and their crosses had been released in the hope of better adaptation, but its occurrence was sporadic and its effect negligible.

In a last desperate attempt, nine parasite species of more or less related graminaceous borers from Africa and Asia were introduced in 1966. All were alien parasites used against a pest native to the Neotropics. One became established (Alam et al. 1971) and produced an unusual success.

Some 2000 individuals of *Apanteles flavipes* Cam. from India, of which 50% were moribund, were released in July 1966. During 1 year or 14 generations, the species could not be traced; but it literally exploded

afterwards: first recoveries were made in October 1967; on 17 October, parasitism in the release site was 22%; on 9 November, 31%; on 11 December, 65%; and on 4 January 1968, already 74%! Simultaneously, a rapid spread occurred: within 3 months, an area of 4 km² was occupied, from where the species was redistributed to speed colonization of the island, which was completed within 1 year.

Simultaneously, populations of *L. diatraeae* increased sharply; apparently an adapted strain had developed after many years of release. The decline of host populations was as spectacular as the increase in parasitism: infestation dropped from an average of 15% to 3–6% within a few years (Figure 1).

As a logical consequence to the outstanding performance of *A. flavipes*, the species was released elsewhere in the Neotropics. To date it has been introduced into 25 countries where only "partial" or "substantial" control have been reported, but nowhere a success similar to that in Barbados [F.D. Bennett, 1985, Biological control of sugarcane borers. *In: Diatraea* spp. in Latin America—an overview (In preparation)]. The *Diatraea* case in Barbados leads to several conclusions, but also poses questions:

1. Inundative releases of *Trichogramma* during some 25 years were unsuccessful. Admittedly, numbers were small, in the order of 300 million
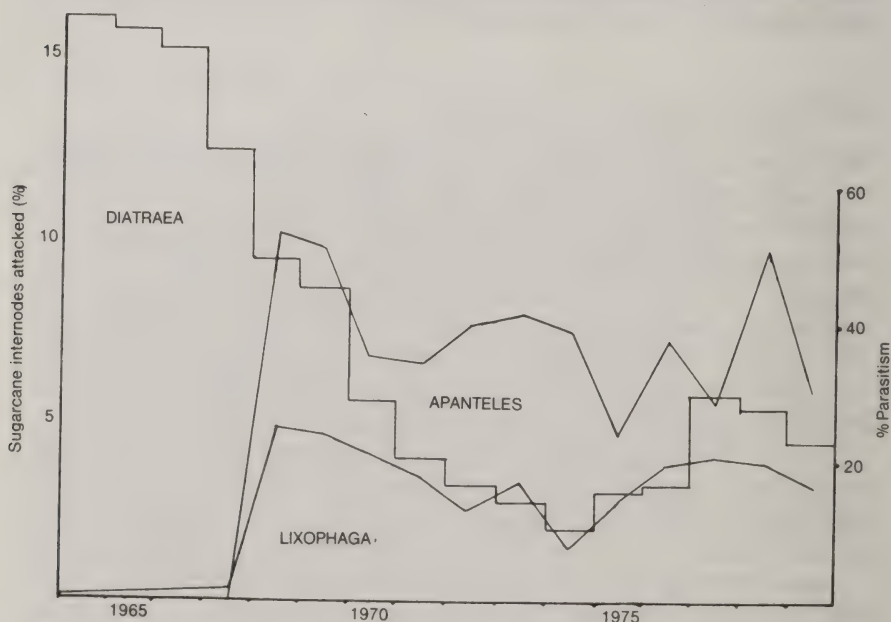
Figure 1. Internodes attacked by *Diatraea saccharalis* (%) in relation to parasitism by *Apanteles flavipes* and *Lixophaga diatraeae* (%), Barbados 1964–79 (after CAB, 1980).

a year in an area of ca. 20 × 30 km. The numbers were considered too small by some, others contended that the wrong species was released. Several other *Trichogramma* release programs at that time failed, but there have been more recent claims of success, e.g., in Russia and China, and in western Europe, where the egg parasites are produced commercially and used against the European corn borer. A better knowledge of the biology and ecology, and the right species or strain to use, are probably the obvious answers to success.

2. The remarkable success of *A. flavipes* in Barbados was unexpected and calls for a reconsideration of theoretical principles of biological control. *Apanteles diatraeae* Mues., a South American species specific to *D. saccharalis*, had been unsuccessfully tried in Barbados and elsewhere in the Neotropics. Both parasites are gregarious and have similar life histories. There is no doubt that in this instance an alien parasite has been superior to an adapted one.

3. *A. flavipes* was released once, in small numbers. The material originated from a culture with presumably reduced genetic variability. Thus success occurred contrary to theory, which calls for large-scale release (Beirne 1984) of parasite material with a broad genetic basis and in various ecological conditions in order to achieve success (Messenger et al. 1976; Mackauer 1972).

4. Why did *A. flavipes* not repeat its success elsewhere in the New World against the same host?

5. *Lixophaga* was released frequently over more than three decades, using several strains and crosses between strains. Establishment had probably already occurred in the 1950s, but a substantial population buildup was not noticed until more than 20 years later. Perseverance in releasing the species, combined with genetic adaptation, appear to be the only plausible answer.

A single outstanding success has brought to light the dilemma of biological control; is it an art or a science? Apparently the performance of a natural enemy is sometimes unpredictable and an alien parasite may be more successful than an adapted native one. Genetic changes adapting *Apanteles* and *Lixophaga* to local conditions must have occurred, and this should lead to a reconsideration of theoretical biological control concepts and release strategies.

Genetics

In both *A. flavipes* and *L. diatraeae*, it appears that there was a phase of adaptation with increasing fitness, apparently by genetic changes. As the numbers of *A. flavipes* were small, and inbreeding had taken place, there was probably not a selection of an adapted genotype from a gene pool with

great variability. But the founder principle formulated by Mayr (1967) offers a more plausible explanation: founding populations (and all intro-duced pests or natural enemies can be regarded as such) pass through a bottleneck of homozygosis where mutations become manifest and, together with genetic drift, lead to new genetic constitutions. This process may sometimes lead to populations with higher fitness.

Although it is likely that the founder principle is applicable to biologi-cal control operations, this has never been tested. A confirmation would not only increase the chances of successful establishment, it would also suggest a change from mass releases to small-scale releases of sub-populations in different habitats.

New Host-Parasite Associations

Pimentel (1963) postulated that alien natural enemies would hold greater promise for the control of a pest than adapted natural enemies, which, due to co-evolution, had reached a state of homeostasis, thereby becoming ineffective. A large number of examples disproves this contention, but the successful control of *Diatraea* by *A. flavipes* and several other examples support the suggestion that alien parasites should be used against native pests. Acceptance of this working hypothesis would greatly enhance the possibilities of exchanging promising natural enemies also of the *Heliothis complex*, e.g., *A. kazak* and *H. didymator* could be transferred from Europe to the Americas, and *Microplitis croceipes* Cresson from America could be used elsewhere.

PREDICTABILITY OF PERFORMANCE OF NATURAL ENEMIES

On the face of it, one would not have considered *A. flavipes* superior to *A. diatraeae*. But if systems become too complex to be dealt with by logical reasoning, they often become the target of modeling. Would this help?

We are all familiar with the life tables developed in the 1950s, which were the basis of the more sophisticated key factor analysis developed by Varley and Gradwell (1968). Morris (1959) developed his single factor analysis based on similar assumptions but reduced the number of parame-ters to be measured: a host population census and one of the natural enemy affecting it. Both of these techniques, more or less tedious, were a good start. But neither these nor the more sophisticated models developed later with systems analysis have so far had an impact on practical biological control.

Considering the short history of modeling, the progress made has been enormous, probably commensurate with the development of ever more powerful machinery, and its benefits to integrated pest management are

undeniable. The currently used model parameters such as searching efficiency, sex ratios, and reproductive rates, are apparently insufficient to describe the performance of a natural enemy in relation to a changing environment. What we need in relation to biological control is more data, and there should be a close cooperation between mathematicians and field ecologists to obtain and process them.

THE ECOSYSTEM AND THE SELECTION OF NATURAL ENEMIES

In a search for parasites of *H. armigera* in Morocco, Spain, Greece, and Bulgaria, only two dominant larval parasites (*A. kazak* and *H. didymator*) were found, besides some accidental primary parasites (*Apanteles* sp. *glomeratus* group, *Temelucha* sp., and *Diadegma picticollis* Thoms.) and two very effective hyperparasites of *A. kazak* and *H. didymator*, the chalcidid *B. secundaria* and the pteromalid *Catolaccus crassiceps* Masi.

Thus, our surveys produced only two of some 12 larval parasites listed as valid species from the Mediterranean Basin in Thompson's Parasite Catalogue. Perkins (personal communication) found in addition two tachinids (*Compsilura concinnata* Mg. and *Exorista segregata* Rond.) at low levels of attack. It is concluded that in large coherent monocultures only the hardiest natural enemies have survived, and that these are the ones with the least requirements regarding adult food and shelter, and are the most resistant to pesticides. They are therefore the most promising biological control candidates to be used in similarly disturbed agroecosystems.

As both of the dominant primary parasites reach high rates of parasitism of 20–60% and are heavily decimated (up to 60%) by hyperparasites, their introduction into New Zealand was recommended. Both species have a shorter life-span than the host, attack and kill early host instars and are considered complementary, although they occupy almost identical parasitological niches.

The main differences between the two species are that *Hyposoter* is more polyphagous than *Apanteles*, and that their host plant selection, which is still incompletely known, varies. The parasites' association with groundnut and tobacco are well established. *H. didymator* is virtually restricted to groundnut, and *A. kazak* to tobacco. *Apanteles* was more common on cotton than was *Hyposoter*, but the complete parasite/host-plant relationships are not yet clear, although of importance in deciding on parasite introductions in relation to individual crops.

A. kazak has been established in New Zealand where it has become an effective control agent on soybean (Cameron & Valentine, these Proceedings). We recommend both species for introduction into areas where they do not occur and where climatic and ecological conditions are not grossly

dissimilar to the Mediterranean Basin, also against related host species such as *Heliothis virescens* (F.). Trial introductions have been commenced by the Southern Field Crop Insect Management Laboratory in Stoneville MS, USA.

Acknowledgments

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Importation and Establishment of New Natural Enemies of *Heliothis* spp. (Lep.: Noctuidae) in Australia

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ABSTRACT

Heliothis punctigera Wallengren and *Heliothis armigera* (Hübner) are serious pests of many crops in three climatic zones in Australia. A large and diverse array of native natural enemies acts against these pests and is very effective under some circumstances. Parasitoids of the large larval and pupal stages are well represented but those attacking earlier stages may be scarce or inconsistent. In tropical Australia, where the climate allows continuous *Heliothis* spp. activity, parasitoids of the egg and early larval stages may be very effective, especially *Trichogramma* spp., *Trichogrammatoidea* spp., and *Microplitis demolitor* Wilkinson. Importations are suggested for the other two climatic zones. *Trichogramma pretiosum* Riley was introduced for augmentative releases in cotton in the tropical and east coast zones. It is established in the release area in the tropics but may have been present prior to the introduction. Parasitoids of the young larval stages have been imported and released in the southern zone. *Campoletis chlorideae* (Uchida) and *Cotesia* (= *Apanteles*) *marginiventris* (Cresson) have been recovered but *Cotesia kazak* (Telenga) and *Hyposoter didymator* Thunberg have not. The program is continuing despite the obstacles of seasonal cropping and discontinuous *Heliothis* spp. activity.

Two species of *Heliothis* are serious crop pests in Australia. The native budworm, *Heliothis punctigera* Wallengren, is the more abundant and widespread species, with a preference for broad-leaved plants, while the corn earworm, *Heliothis armigera* (Hübner), is attracted to graminaceous as well as broad-leaved crops (Wardhaugh et al. 1980; Wilson 1982; Twine, these Proceedings). The classical importation of natural enemies of *Heliothis* spp. has not been attempted in Australia until recently (Michael et al. 1984), and there is a heavy reliance on chemical control (Wilson 1982; Goodyer et al. 1984).

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A comparison of *Heliothis* spp. natural enemies in Australia with those in other countries would indicate few empty niches, but Greathead and Girling (1982) observed the absence of certain genera. This paper suggests that importations are desirable to fill gaps in certain areas and crops and describes a program aimed at establishing four new parasitoids.

NATIVE NATURAL ENEMIES

Climate and Crops

The great differences in climate and cropping patterns in Australia have a profound effect on the activity of *Heliothis* spp. (Wilson 1982) and the effectiveness of their natural enemies. Three major climatic zones may be recognized.

In tropical Australia, the hot months are rainy and the cooler months are generally dry. Both *Heliothis* species are active throughout the year, especially where crops are irrigated in the dry season. Damaging infestations may be found after a period of adverse conditions in the cropping area (Titmarsh 1980a).

The east coast zone is marked by a predominantly summer rainfall and colder winters, especially with increasing latitude. The great majority of crops susceptible to *Heliothis* spp. is grown in this area and both species exploit a succession of crops grown through the warm months (Wardhaugh et al. 1980). There is little winter activity of *Heliothis* spp. and both species are known to diapause.

Across southern Australia the rain falls predominantly in the winter, which is too cold for *Heliothis* spp. activity. The conditions in this zone do not favor *H. armigera*, which is absent from the most southerly parts, but large numbers of *H. punctigera* appear in the spring (Cullen 1969). Summer crops are of less importance in this zone, compared with the large areas of crops or pasture which mature in the spring or early summer, such as peas, lupins, legume-based pastures, and cereals.

Predators

Numerous general predators are found in association with *Heliothis* spp. on cotton (Bishop and Blood 1977). Although Room (1979) showed that many of these feed on *Heliothis* spp., and a direct relationship was found between two spider species and *Heliothis* spp. (Bishop and Blood 1981), estimates of their total effect are crude (Ives et al. 1984).

One predator that is not present in cotton is *Orius* sp., although it is present on sunflowers (Wilson 1982). It is unlikely that importations of an effective *Orius* sp. or any other predators will be considered in the short term.

Pathogens

Five diseases of *Heliothis* spp. occur in Australia (Teakle 1977). The nuclear polyhedrosis virus (NPV) is the most effective of these and is common on several crops (Teakle 1977; Bishop 1984). An importation of a commercial preparation of the NPV was tested and shown to have an equivalent potency to the Australian species as material from *H. punctigera* (Teakle 1979). The NPV from *Autographa* sp. was considered as another possible importation.

Parasitoids

The parasitoids are considered here in greater detail as current importations involve parasitoids and this is likely to be the case with future importations of natural enemies. A list of native parasitoids is given in Table 1.

Table 1. Native parasitoids of Heliothis *spp. in Australia*

Parasitoid	*Heliothis* stage at death
Hymenoptera: Trichogrammatidae	
Trichogramma australicum Girault	Egg
Trichogramma chilonus Ishii	Egg
Trichogramma sp. nr. *ivelae* Pang and Chen	Egg
Trichogramma pretiosum Riley	Egg
Trichogrammatoidea flava Girault	Egg
Trichogrammatoidea nana Zehntner	Egg
Paratrichogramma heliothidis Viggiani	Egg
Trichogrammanza funiculatum Carver	Egg
Hymenoptera: Scelionidae	
Telenomus sp. nr. *triptus* Nixon	Egg
Hymenoptera: Braconidae	
Cardiochiles sp.	Small larva
Chelonus (*Microchelonus*) sp.	Small larva
Microplitis demolitor Wilkinson	Small larva
Microplitis sp.	Small larva
Rogas sp.	Small larva
Hymenoptera: Ichneumonidae	
Heteropelma scaposum (Morley)	Pupa
Lissopimpla excelsa (Casta)	Pupa
Netelia producta (Brulle)	Large larva
Pterocormus promissorius (Erichson)	Pupa
Diptera: Tachinidae	
Carcelia cosmophilae (Curran)	Large larva
Carcelia illota (Curran)	Large larva
Chaetophthalmus dorsalis (Malloch)	Large larva
Exorista curriei (Curran)	Large larva
Goniophthalmus australis (Baranov)	Pupa

Several species of egg parasitoids have been recorded from *Heliothis* spp. (McLaren and Rye 1981; Nagarkatti and Nagaraja, personal communication; Subba Rao, personal communication; Viggiani 1976). Different levels of parasitism are found in different areas and crops. In tropical Australia, over 90% of eggs were frequently parasitized in sorghum and cotton by *Trichogramma* spp. and *Trichogrammatoidea* spp. (Michael 1973; Michael and Woods 1980). In the east coast zone, Twine (1973) found generally low levels of parasitism by three species, with the most important being *Telenomus* sp. At a somewhat higher latitude, parasitism was very low in cotton crops (Wilson 1982).

Of the parasitoids which destroy small larvae, only *Microplitis* spp. are effective. *Microplitis demolitor* Wilkinson is probably the important species in all three climatic zones. In the tropical north, well over 50% parasitism by *Microplitis* spp. was frequently recorded in tobacco (Titmarsh 1980b). Also in the tropical north, *Microplitis* sp. (= *Microgaster* sp.) was very effective and, together with egg parasitoids, sometimes destroyed all *Heliothis* spp. larvae in sorghum before the fifth instar (Michael 1973). *Microplitis* sp. was the most effective parasitoid in sunflowers (Broadley 1984).

Several other parasitoids affecting small larvae are present but are ineffective. These include *Cardiochiles* sp. and three unidentified species in cotton (Room 1979), *Rogas* sp. in lucerne (Bishop 1984), and *Chelonus* (*Microchelonus* sp.) in sunflower (Broadley 1984).

Many parasitoids have been reared from large larvae or pupae of *Heliothis* spp. Fourteen tachinid parasitoids are known and the taxonomy has been clarified so that the five species listed in Table 1 are known to be the most effective (Cantrell 1984, 1985a, 1985b; personal communication). Several ichneumonid parasitoids are present throughout the range of environments but *Heteropelma scaposum* (Morley) is the most effective (Room 1979; Shepard et al. 1983; Broadley 1984).

Parasitoid Deficiencies

Parasitoids which destroy late instar larvae or pupae are well represented in Australia by several effective tachinids and ichneumonids. However, high mortality of early stages is more desirable for immediate crop protection and it is for these stages that effective parasitoids are required.

Under the conditions of continuous *Heliothis* spp. activity in tropical Australia, egg and early-larval parasitoids are frequently very effective. Moving away from the tropics, there is a decreasing level of parasitism of the early host stages. The same parasitoids that are effective in the tropics are not able to maintain high numbers with the seasonal nature of cropping and host activity. This limiting factor may be partially overcome by

parasitoids with a high rate of increase and a mechanism to bridge the inactive period, such as the diapause known in some native parasitoids (Kay 1982). An alternative strategy is to employ less specific parasitoids that are able to use other available hosts.

Greathead and Girling (1982) noted the absence from Australia of *Apanteles* spp., *Bracon* spp., and *Chelonus* spp. Even though a *Chelonus* sp. has now been located, all of these are still worth considering for importation. To these could be added *Campoletis* spp. and *Hyposoter* spp.

Cotton suffers more from attack by *Heliothis* spp. than any other crop (Wilson 1982) and resistance to insecticides is a major problem (Goodyer et al. 1984). Egg parasitoids have little effect, especially in the higher latitudes, and suitable candidates could be imported. Even the native *Microplitis* spp. seem to be ineffective in cotton although a very successful species is found in cotton in the USA (Smith et al. 1976; King et al. in press). Importations of parasitoids attacking early instars should be considered. Factors working against the achievement of good biological control in cotton include the costly damage caused even by young larvae and the other serious pests which must be controlled. Other high-value crops such as tomatoes suffer the same problems.

A more promising situation exists with other crops such as sunflowers and sorghum, which are not as sensitive to attack and which have fewer serious pests. For these reasons lupins are ideal for biological control. Economic damage only results from large larvae feeding on the maturing pods (Michael et al. 1982). This crop has few other pests and disruptive chemical control is rarely required. Moreover, the lupin crops are surrounded by large unsprayed areas of legume-based pasture and cereal crops. In southwest Australia alone, there are half a million hectares of lupins interspersed with seven million hectares of pasture and six million hectares of cereal crops (Australian Bureau of Statistics 1985).

NEW NATURAL ENEMIES

Importations

The parasitoids introduced into Australia for the control of *Heliothis* spp. are shown in Table 2. The earlier introductions of *Trichogramma pretiosum* Riley were for cotton in the east coast and tropical areas, whereas all the recent importations are part of a continuing program to establish new natural enemies against noctuid pests in southern Australia (Michael et al. 1984). Apart from *Heliothis* spp., the target pests are armyworms, *Mythimna* spp. (= *Pseudaletia* spp.) and *Persectania* spp.; cutworms, *Agrotis* spp.; and cluster caterpillars, *Spodoptera* spp.

Table 2. Parasitoids of Heliothis *spp. imported into Australia*

Parasitoid	Origin	Year imported
Hymenoptera: Trichogrammatidae		
Trichogramma pretiosum Riley	USA	1973, 1974, 1975
Hymenoptera: Braconidae		
Cotesia (= *Apanteles*) *marginiventris* (Cresson)	USA	1982
Cotesia (= *Apanteles*) *Kazak* (Telenga)	Greece	1983, 1985
Hymenoptera: Ichneumonidae		
Campoletis chlorideae (Uchida)	Pakistan	1982, 1983
Hyposoter didymator Thunberg	Greece	1983, 1985

T. pretiosum was imported from the USA in 1973–75 to determine the effectiveness of augmentative releases in cotton rather than to establish a new natural enemy (Michael and Woods 1980; Twine and Lloyd 1982). *T. pretiosum* has commonly been used for such programs and has been effective in some cases (Oatman and Platner 1971).

The other introduced parasitoids were shipped from field stations of the Commonwealth Institute of Biological Control in Pakistan, Trinidad, and Switzerland and from the Department of Scientific and Industrial Research, New Zealand. They were received into quarantine at the Department of Agriculture, Perth (Michael et al. 1984).

Campoletis chlorideae (Uchida) is the most effective parasitoid of *H. armigera* in India (Rao 1974). It is widespread and is found at all times of the year on a wide variety of hosts. It is heavily parasitized by several hyperparasites. Cross-mating studies showed that *C. chlorideae* is different from *Campoletis sonorensis* (Cameron) but the two are similar in many respects (Lingren et al. 1977).

Cotesia (= *Apanteles*) *marginiventris* (Cresson) is a useful parasitoid of *Heliothis* spp. in the USA, especially in the early part of the season (Pair et al. 1982). It is not specific to *Heliothis* spp. but has a wide host range (Boling and Pitre 1970; McCutcheon and Turnipseed 1981).

Hyposoter didymator Thunberg and *Cotesia* (= *Apanteles*) *kazak* (Telenga) are significant parasitoids of *H. armigera* over at least part of their geographic range and on several host plants (Carl 1976, 1978). *C. kazak* is thought to be specific, but *H. didymator* is a common parasitoid of several other hosts (Gerling 1969; Ingram 1981). In Israel, *H. didymator* is an effective early-season parasitoid of *H. armigera* on cotton (Bar et al. 1979). Both parasitoids may themselves be heavily parasitized (Carl 1976).

C. kazak was forwarded to New Zealand where it was recovered 2 years after the last release (Singh et al. 1982). It has since continued to spread (CIBC 1984).

Rearing and Release

In 1973–74, *T. pretiosum* from Rincon-Vitova in California was released

in the subtropical east coast area into cotton at the rate of 80,000 per week (Twine and Lloyd 1982). The following season material from the same source was released in 200 ha of cotton in the tropical zone at approximately the same rate (Michael and Woods 1980). Parasitized eggs were then collected from release sites in the tropical zone and a parasitoid colony established. Grimm and Lawrence (1975) developed some novel mass-rearing methods, using *Sitotroga cerealella* (Olivier) as the host, and shipped the parasitoid to the same two areas, where it was released at the rate of approximately 50,000 per week.

Several noctuid species were maintained on a synthetic diet modified from Shorey and Hale (1965) for rearing the imported larval parasitoids (Michael et al. 1984). Mass rearing of parasitized larvae was possible with most noctuid species.

Preliminary host testing showed that the two ichneumonid parasitoids had a wide range of hosts in which they readily oviposited and developed normally. *C. marginiventris* had a narrower host range and *C. kazak* was very restricted.

Parasitoids were released as mated adults in the southern and tropical climatic zones in areas where host larvae were known or thought likely to be present. Up to June 1984, some thousands of the earlier introductions and hundreds of the later introductions had been released (Michael et al. 1984).

Establishment

A *Trichogramma* sp. close to *T. pretiosum* but variously identified as *Trichogramma australicum* Girault or *Trichogramma* sp. group *T. pretiosum–T. minutum* was highly successful in tropical Australia prior to the importation of material from the USA. Three years after the importation, material from the release site was forwarded to the USA, where cross-breeding studies showed it to be *T. pretiosum* (Oatman and Platner, personal communication). It is possible that the native species was displaced in that area or that *T. pretiosum* was already present. Collections over a wider area and further cross-breeding studies would be needed to determine the true situation. It may be of significance that eggs of *Anomis* spp. were heavily parasitized in the tropical zone but not in the east coast zone (Michael and Woods 1980; Twine and Lloyd 1982).

Of the larval parasitoids of *Heliothis* spp., only *C. chlorideae* and *C. marginiventris* have been recovered in low numbers (Michael et al. 1984). Both species have been found in irrigated areas but not in raingrown crops. *C. chlorideae* was reared from *H. punctigera* on lucerne and *C. marginiventris* was reared from *Spodoptera litura* (F.) on weeds.

Specific determinations of *Campoletis* spp. have been difficult, although only two Australian species are known (Gauld 1984). *Campoletis*

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sp. has not previously been reared from *Heliothis* spp. but the introduced species readily oviposits in *H. punctigera* in the field.

These initial results are not greatly encouraging but the program is continuing, and there is hope for further recoveries and establishment. These or similar species should be introduced into the east coast area where the summer rains and greater diversity of summer cropping lead to greater *Heliothis* spp. activity.

It is perhaps meaningful that the only recoveries from the southern climatic zone have come from irrigated areas. The extreme seasonality of lupins and other nonirrigated agriculture is a major obstacle against successful biological control. Not only are *Heliothis* spp. active for a shorter period than in the other two climatic zones, but the crops mature early in the season and this is followed by a prolonged dry period.

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Importation and Establishment of New Natural Enemies of *Heliothis* spp. (Lep.: Noctuidae) into India

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ABSTRACT

In spite of the numerous parasite species attacking *Heliothis armigera* (Hübner) in all life stages, it continues to be a major pest of fiber and food crops in India. From about 1969 onwards, efforts have been made to introduce and establish egg, egg-larval, and larval parasites; these include the hymenopterans, *Trichogramma* spp., *Chelonus* spp., *Cotesia* (= *Apanteles*) *marginiventris* (Cresson), *Microplitis croceipes* Cresson, and *Campoletis flavicincta* (Ashmead), and the dipterans, *Lespesia archippivora* (Riley) and *Eucelatoria bryani* Sabrosky. Of these parasites, *Chelonus blackburni* Cameron and *E. bryani* have been established, but their population levels are so low that they probably have little economic impact. Also, species of the egg parasite *Trichogramma* have been temporarily established. The parasites *Chelonus insularis* (Cresson) and *C. flavicincta* could not be colonized for introduction because no females or not enough females were available under laboratory conditions. Other parasites targeted for introduction include *Cotesia* (= *Apanteles*) *kazak* Telenga and *Hyposoter didymator* Thbs. from Europe. It is recommended that future introductions focus on egg parasites that are less selective of host plants and parasites (e.g., *M. croceipes*) that attack early larval instars. Parasitization of early-stage lavae may limit feeding on the plant to nonfruiting structures. Also, more effort should be made to import parasites from Central and South America, northern Australia, Africa, and southern Europe, because they may be better suited to Indian conditions. Moreover, greater emphasis should be placed on large founder colonies with high genetic variability to ensure establishment. It may be important to import large numbers of *M. croceipes* and *C. marginiventris* adults for direct field colonization rather than increase their numbers in the laboratory after receipt of a few individuals.

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The economic importance of *Heliothis armigera* (Hübner) in India has been sufficiently documented in other papers within this book and the inability of the large complex of natural enemies to maintain the pest below economic levels in India is self-evident. There are numerous reasons for the increased impact of *H. armigera* on various crops in India. These include an increase in the area planted to susceptible crops, meteorological and other changes in the last few decades that may have been to the disadvantage of natural enemies, and possibly the abundant growth of weeds which serve as alternative hosts. Reed and Pawar (1982) were of the opinion that pesticide usage in India is too low to affect the population dynamics of *H. armigera*. However, they believed that increased use of irrigation in south India increased the availability of host plants through the dry season. Consequently, pest numbers increased on the irrigated crops and dispersed northward. These factors, along with inherent characteristics of the indigenous natural enemies, often render natural (biological) control ineffective.

While it is possible that conservation of indigenous natural enemies and better cultivation practices combined with the use of selective pesticides may be the ultimate answer to successful control of *H. armigera*, we believe that the introduction of exotic natural enemies may be important. There may be an additive to the present level of parasitism, possibly through occupation of vacant niches (even though these may not as yet be clearly defined). Also, it may be possible to establish natural enemies which possess high levels of pesticide tolerance. We refer here only to introduction of natural enemies against *H. armigera*, since *H. peltigera* Denis and Schiffermüller and *H. assulta* (Guenée), though present in India, are not of economic importance.

During the last two decades, exploratory surveys in India for parasites and predators of *Heliothis* spp. by the Indian Station of the Commonwealth Institute of Biological Control (CIBC) at Bangalore and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at Hyderabad have indicated that although numerous natural enemies are present, only a few are important. Commencing in 1969, the CIBC station made efforts to introduce egg, egg-larval, and larval parasites of *H. armigera* into India. These efforts have been continued under the All India Coordinated Research Project on Biological Control of the Indian Council of Agricultural Research and the biological control project of the Directorate of Plant Protection, Quarantine and Storage.

NATURAL ENEMIES IMPORTED INTO INDIA

Egg Parasites

The only egg parasites introduced into India specifically against *H.*

Table 1. Egg and egg-larval parasites of H. armigera *introduced into India*

Species	Origin	Year of introduction	Establishment[1]
Hymenoptera			
Trichogrammatidae			
Trichogramma brasiliensis Ashmead	S. America	1968 & 1982	X
T. perkinsi Girault	S. America	1966	X
T. pretiosum Riley	USA & Mexico	1968	X
Braconidae			
Chelonus blackburni Cameron	USA	1976	+
C. insularis Cresson	West Indies	1982 & 1983	#

[1]X = no permanent establishment; + = established at low levels; # = colonization not possible.

armigera (Table 1) thus far are the Trichogrammatidae, *Trichogramma brasiliensis* (Ashmead) (origin: S. America), *T. perkinsi* Girault (origin: USA), and *T. pretiosum* Riley (origin: Mexico and USA). Even these introductions were made as an off-shoot of a U.S. PL-480 project on taxonomic studies of the genus *Trichogramma*, under which numerous live cultures were obtained from around the world. In addition to releases made by CIBC, nucleus cultures were supplied to various organizations in the country, such as the Indian Agricultural Research Institute (IARI), New Delhi; the All India Coordinated Sorghum Improvement Project at Hyderabad; Marathwada Agricultural University at Parbhani; the University of Agricultural Sciences at Dharwad; Punjab Agricultural University; Ludhiana; and Gujarat Agricultural University, Anand. These in turn multiplied the *Trichogramma* spp. and colonized them in crops such as cotton, sorghum, maize, pulses, beans, tomato, and okra. In trials conducted by IARI in cotton, it was reported (Sangwan et al. 1972) that 89% of bollworm eggs were parasitized by *T. brasiliensis*. At the Indian Institute of Horticultural Research (IIHR) in Hessaraghatta, *T. brasiliensis* and *T. pretiosum* were released at 7-day intervals from the time of fruit set on tomato. The percentage of *Heliothis*-damaged fruits was 9.52 compared with 21.7 in the untreated plot (Anon. 1974).

Nevertheless, despite massive efforts at colonization of *Trichogramma* spp. by the above organizations and the Central Biological Control Stations operating under the Directorate of Plant Protection, Quarantine and Storage, there has been no evidence of permanent establishment in India of any of the exotic species. Moreover, it has been found (Bhatnagar and Davies 1978) that the acidic exudates on pigeonpea and chickpea have a repellent effect on *Trichogramma* spp., resulting in poor parasitism of *H. armigera* eggs.

Egg-larval Parasites

Efforts to introduce egg-larval parasites of *H. armigera* were commenced
in 1976 by the CIBC. *Chelonus blackburni* Cameron was imported from
the USA and colonized in the laboratory on eggs of the rice moth, *Corcyra
cephalonica* Stainton, and the potato tuber moth, *Phthorimaea opercu-
lella* (Zeller). Initially, about 300 adults were released near Bangalore, in a
bean field infested with *H. armigera*. Later, stocks were also obtained by
the CIBC from Hawaii. In the Marathwada area, recoveries were reported
from *H. armigera* by Sarkate et al. (1978). More recently, Pawar et al.
(1983) reported the release of over 5000 adults of *C. blackburni* in cotton
fields with mixed populations of *H. armigera*, the pink bollworm (*Pecti-
nophora gossypiella*), and the spotted bollworm. The actual impact of the
parasite on *H. armigera* alone cannot be assessed from data provided by
the above authors. They placed *C. cephalonica* eggs in the field to recover
C. blackburni, although up to 25% parasitism of the latter host was
recorded. Moreover, since dates of releases and recoveries overlap, per-
manent establishment of the parasite in Haryana State cannot be sup-
ported by the data. The parasite has also been released in the Pune area
against potato tuber moth and recovered (Choudhary et al. 1983). So it
appears that the parasite is established in some parts of India.

Three shipments of *Chelonus insularis* (= *texanus*) (Cresson) were
obtained from Trinidad (West Indies) by the IIHR during 1982 and 1983.
Only males emerged from these shipments; hence no studies were possible.

Larval Parasites

The larval parasites listed in Table 2 have been imported into India during

Table 2. Larval parasites of H. armigera *introduced into India*

Species	Origin	Year of introduction	Establishment[1]
Hymenoptera			
Braconidae			
Microplitis croceipes Cresson	Arizona, USA	1970	Not known
Cotesia marginiventris Cresson	Arizona, USA	1969 & 1981–1983	–
Ichneumonidae			
Campoletis flavicincta Ashmead	Trinidad, West Indies	1981	#
Diptera			
Tachinidae			
Eucelatoria bryani Sabrosky	Arizona, USA	1969, 1978	+
Lespesia archippivora Riley	Arizona, USA	1969, 1970	–

[1]+ = established at low levels; – = not established; # = colonization not possible.

the past two decades for trials against *H. armigera.* No benefit has been obtained from release of these parasites.

Hymenopterous larval parasites introduced include *Microplitis croceipes* (Cresson) and *Cotesia marginiventris* (Cresson) from Tucson, Arizona. The former was obtained from the U.S. Department of Agriculture in 1970, and one generation was bred in the CIBC laboratory on *H. armigera.* However, no details are available on further multiplication or field releases, so the culture was apparently lost.

C. marginiventris was first obtained in 1969. It readily attacked young larvae of *H. armigera* and *Spodoptera litura.* One hundred and thirty-five mated females were released in an infested tomato field at Whitefield, near Bangalore (Rao et al. 1971). No recoveries are reported by CIBC. Stocks of *C. marginiventris* were again obtained in 1981 by IIHR and multiplied primarily on *S. litura* in the laboratory because of difficulty in maintaining virus-free *H. armigera* cultures. Initially, the sex ratio was so highly in favor of males that only a small colony could be maintained. The situation gradually improved by 1982, enabling shipments of the parasite to Gujarat Agricultural University at Anand, where it was multiplied. A small colony of 15 females and 20 males was released in a groundnut field infested with *S. litura* during October 1983, but no recoveries have been reported. Cocoons of *C. marginiventris* were also supplied to the Central Tobacco Research Institute in Rajahmundry (Andhra Pradesh), where also the species was multiplied on *S. litura.* Between September and December 1983, over 5,000 adults were released in tobacco and vegetable fields, but to date the parasite has not been recovered.

However, O'Connor (1960) has reported that in Fiji *C. marginiventris* imported from Hawaii against *Mythimna separata* (Walker) became well established throughout the island of Viti Levu and prevented serious outbreaks of the pest. This establishment occurred despite the presence of many native secondary parasites.

Four shipments of *Campoletis flavicincta* (Ashmead) were received by IIHR from CIBC West Indian Station during 1981. There was a preponderance of males among adults that emerged. The shortage of female progeny, plus a bacterial disease in the parasitized *H. armigera* larvae, prevented the establishment of a culture and colonization.

With the reported success of *Cotesia kazak* Telenga, introduced from Bulgaria into New Zealand, permission was obtained to import this species into India along with another European species, *Hyposoter didymator* Thbs. Neither of these parasites has been tested yet, but it is anticipated that *C. kazak,* particularly, may establish. Reasons for this optimism include the ability of *C. kazak* to perform well even when host density is low, the fact that it has no obligatory diapause, and the insecticide tolerance it exhibits.

During 1969, CIBC (Anon. 1969) obtained a culture of the tachinid *Lespesia archippivora* (Riley) from the U.S. Department of Agriculture in Tucson, Arizona. In the laboratory, *L. archippivora* did not develop on *H. armigera*, *S. litura* F., or *Archaea janata* (L.) although Butler (1958) had reported it to have a broad host range. Subsequently, 565 mated females of *L. archippivora* that emerged from puparia received from Arizona were released in tomato fields at Sunkadakatte near Bangalore. Also, 200 flies were released at Coimbatore in Tamil Nadu. No recoveries of this parasite have been reported from any Noctuidae in India.

In 1969, CIBC first imported the tachinid *Eucelatoria bryani* Sabrosky for trials against *H. armigera*. A total of 153 mated females was released in infested tomato fields in Hoskote and Whitefield (near Bangalore) and 139 mated females were released in bean (*Dolichos lablab*) at Sunkadakatte. Forty mated females were also released in chickpea fields at Pipariya (Madhya Pradesh) (Rao et al. 1971). Although 2 of 38 larvae collected 10 days after colonization of the tachinid were found parasitized by this species (Anon. 1969), it was not recovered again in the Bangalore area. There is no information on recoveries at Pipariya.

In 1978, the Central Biological Control Stations requested stocks of *E. bryani* from CIBC, and four shipments were obtained from the U.S. Department of Agriculture at Stoneville, Mississippi. Because of delays in transit, only 25 adults were received alive. Of these, seven mated females enabled establishment of a laboratory colony (Sankaran and Nagaraja 1979). Between January 1979 and April 1980, 1560 *E. bryani* flies and 798 larvae parasitized by the tachinid were released in Bangalore district (Pawar et al. 1981). In January 1979, these authors reported that 30 *H. armigera* larvae were collected from a mixed crop of pigeonpea and beans exposed to *E. bryani* females, and these, together with 10 mated females, were released in the field. Two weeks later, 30 larvae were collected at random and 5 of these were found parasitized. Subsequently, Pawar et al. (1981) reported that additional *H. armigera* larvae, collected from tomato fields where the parasite had been released earlier, yielded *E. bryani* puparia. This work indicated that *E. bryani* is capable of surviving and propagating under Bangalore conditions. Mishra et al. (1982) reported that *E. bryani* gave 0.3–0.8% parasitism in the Gorakhpur area of eastern Uttar Pradesh following releases; however, no evidence of permanent establishment in this area has been provided.

Sithanantham and Reed (1980) reported that in field-cage studies at ICRISAT, Hyderabad, release of *E. bryani* in pigeonpea and chickpea resulted in 14.2% and 4% parasitism, respectively. These higher rates of parasitism could have been due to the flies being confined in field cages. In a subsequent report, ICRISAT entomologists reported that even after 40 generations were reared in the laboratory, *E. bryani* appeared to be biologically unchanged (Anon. 1982). Nevertheless, efforts to raise a strain

tolerant of high temperatures were in progress. During 1981–82, colonization of the tachinid resulted in 6.9%, 2.0%, 1.4%, and 4.3% parasitism of *H. armigera* larvae in chickpea, millet, sorghum, and pigeonpea, respectively.

With the commencement of the All India Coordinated Research Project on Biological Control (AICRPBC), efforts to multiply *E. bryani* and test its ability to establish in and around Bangalore and other areas have continued. In 1980–81, 573 females were released in tomato fields in and around Anand. Initially, only 2 *H. armigera* larvae, collected on cotton, were found parasitized by *E. bryani* (Anon. 1983). Releases of laboratory-bred *E. bryani* were also commenced in 1980 by entomologists at the IIHR in and around Hessaraghatta. Mani and Krishnamoorthy (1983) reported that 190 mated females were released in tomato fields at Shivakote. Also, 90 *H. armigera* larvae parasitized by *E. bryani* were placed on the plants. (We speculated that release of parasitized host larvae might enhance the probability of establishing the parasite.)

The second release site was at Ivarakandapura. There, mated *E. bryani* were released in a tomato field containing *H. armigera* larvae, which had been artificially infested. At the third release site in Bedrahalli, 75 mated females were released in 1981, with 100 mated females at the fourth release site in Thavarekere during 1981. The parasite was recovered only from host larvae (515) collected at Shivakote. Parasitism ranged from 0–8.0%. Since recoveries were made even as much as 14 months after releases at Shivakote, it was evident that the parasite was at least temporarily established.

Studies at IIHR have shown that certain pesticides such as quinalphos and the pyrethroid permethrin are highly lethal to *E. bryani*. So, indiscriminate use of these in or near release sites may delay or even prevent establishment of the tachinid (Mani and Nagarkatti, in press).

DISCUSSION

An evaluation of progress achieved in introducing natural enemies of *H. armigera* into India and planning for future introductions are appropriate. For reasons not fully understood, none of the exotic *Trichogramma* spp. have become permanently established. Large numbers of the parasites were released in the field at the most appropriate stage of the crop in the presence of abundant host eggs. Either characteristics inherent in the exotic species, interspecific competition with the indigenous species, and/or unfavorable microclimatic differences appear to be responsible for the nonestablishment of these parasites.

Among the indigenous Trichogrammatidae, *T. chilonis* Ishii appears to be best adapted to local conditions. Since the exotic *Trichogramma* have been released in sufficiently large numbers and in different ecological areas of the country, there seems little justification for continuing efforts

with these egg parasites. Moreover, the inability of *Trichogramma* spp. to parasitize host eggs on major host crops of *H. armigera* such as pigeonpea and chickpea further reduces justification for more trials. *T. brasiliensis*, however, is a good candidate for augmentative releases (being uniparental) in crops like cotton, vegetables, and cereals. Introduction of the scelionid egg parasite *Telenomus* sp. nr. *triptus* Nixon from Australia should be considered, because scelionids are generally known to be highly specific and therefore are more likely to produce a direct impact on the target pest.

Many factors may be responsible for the failure of *E. bryani* to increase in India. The small founder colony may have had a role in reducing genetic variability of the adults released. The same tachinid was introduced into the Caribbean islands to Grenada, St. Vincent, Antigua, Barbados, St. Kitts, St. Lucia, Dominica, and Trinidad in 1972, but no recoveries were reported (Yaseen 1978). Whether *E. bryani* will build up to economic levels in India in the near future is debatable. It is possible that *E. bryani* may perform better in areas with cold winters similar to those in the southern USA. This would allow for slower development in the winter and better synchrony with the host. Competition with local tachinids may be playing a role in low parasitism levels by *E. bryani*. Colonization of *H. armigera* by *E. bryani* in okra may enable quicker establishment since it is more attractive as a host plant habitat than cotton, according to Nettles (1979).

Scant effort has been made to introduce and establish *M. croceipes* in India. However, in view of its importance as a *Heliothis* parasite in the USA (Bryan et al. 1969), its ability to attack all larval instars of the host (Lewis 1970), and the reduction in feeding damage caused by parasitized host larvae (Hopper and King 1984), greater effort should be directed towards *M. croceipes*. King et al. (1985) suggested that *M. croceipes* may be a candidate for augmentative releases.

In view of the poor results obtained so far with parasites introduced from North America, future efforts should be directed toward introductions from other more subtropical and tropical regions. Parasites from these areas may be better suited for establishment in south and central India. However, species from northern Africa and southern Europe may be better suited to conditions prevailing in north India. It would also seem logical to obtain *H. armigera* parasites from the African continent, particularly since introductions in the reverse direction, from India into East Africa, have shown promise. Greathead (1971) reported that *Campoletis chlorideae* Uchida (earlier thought to be *C. perdistinctus* (Viereck)) was recovered on a number of occasions after colonization. However, details of parasitism and overall impact on the pest are not available.

It is contended (Anon. 1978) that classical biological control of *H. armigera* is not very feasible because of the migratory (long-range dispersal) behavior of moths and their ability to rapidly increase in population

levels. Also, if Turnbull and Chant's (1961) theory is considered, the fact that *H. armigera* behaves at times as an indirect pest (feeding on leaves and flower buds of pulse plants) and later as a direct pest (feeding on the fruiting bodies) may make it more difficult to achieve control using inoculative releases of exotic natural enemies. This would be particularly true for those parasites which attack the later larval instars. For this reason, it would seem necessary to introduce egg and egg-larval parasites, because they are capable of killing the pest in the early life stages before extensive damage occurs.

The introduction of *M. croceipes* and hymenopterous parasites of *Heliothis* spp. with similar habits is justified. Efforts to establish *C. marginiventris* should be continued. With the latter species, it may be necessary to obtain additional (perhaps field-collected) material for direct field release in India to ensure the presence of an acceptable sex ratio and greater genetic variability.

In conclusion, we would like to draw attention to Hussey's (1985) statement that lack of sufficient investment leads to costly mistakes in classical biological control. One cannot overemphasize the need for adequate financial support for exploratory surveys in other countries as well as the other steps in the sequence that determines success in a biological control program.

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Importation and Establishment of Predators and Parasitoids of *Heliothis* into the USA

J.E. Powell*

ABSTRACT

The hemipteran predators *Paratriphleps laeviusculus* Champ., *Sycanus indagator* (Stål), and *Pristhesancus papuensis* Stål were imported into the USA and evaluated for suppression of *Heliothis* spp. None ever became established. More extensive parasitoid programs have resulted in importation of at least 17 species from 7 countries for testing on *Heliothis* spp. Species currently being studied are the braconids *Cotesia kazak* (Telenga), *Microplitis demolitor* Wilkinson, and *M. rufiventris* Kok, the ichneumonid *Hyposoter didymator* (Thunb.), and the tachinid *Palexorista laxa* (Curran).

Recent literature that discusses importation for biocontrol of *Heliothis* spp. in the USA includes Johnson et al. (1986), King et al. (1986), Shepard and Herzog (1985), Jones et al. (1985), and King et al. (1982). Natural enemies were first imported into the USA for biological control of *Heliothis* spp. in the late 1940s (Johnson et al. 1986). Over the next 30 years, natural enemies were received at the U.S. Department of Agriculture quarantine station in the Northeast, now called the Beneficial Insects Research Laboratory and located in Newark, Delaware. This station processed the insects and forwarded them to destination states for field release against target pests. Since the late 1970s, many biocontrol programs have imported natural enemies through the Stoneville Research Quarantine Facility (SRQF) in Stoneville, Mississippi. SRQF is operated from within the U.S. Department of Agriculture Southern Field Crop Insect Management Laboratory.

Currently, 20 state and federal facilities act as quarantine receiving centers for exotic beneficial organisms in the USA, but the one most actively involved in importing natural enemies of *Heliothis* spp. is SRQF.

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Table 1. Predators of Heliothis spp. imported into the United States of America

Species	Origin	Year(s) shipped	Destination states
Hemiptera: Anthocoridae			
Paratriphleps laeviusculus Champ.	Peru	1941–42 1958	Texas
Hemiptera: Reduviidae			
Sycanus indagator (Stål)	India	1967	Georgia, Louisiana, Mississippi
Pristhesancus papuensis Stål	Australia	1978	South Carolina

IMPORTED NATURAL ENEMIES OF *HELIOTHIS*

Predators

Only three hemipteran predators have been imported for control of *Heliothis* spp. (Table 1). The first, *Paratriphleps laeviusculus* Champ., imported from Peru, was released in the field in Texas, but did not become established (Clausen 1978). Potential of the two reduviids (Table 1) was studied in the laboratory (Johnson et al. 1986). Even though *Sycanus indagator* (Stål) from India and *Pristhesancus papuensis* Stål from Australia were capable of attacking *Heliothis* spp. larvae, these species were never established in the field.

Parasitoids

The parasitoids imported from India during the 1950s and 1960s are listed in Table 2. Many of these were originally targeted for suppression of *Pectinophora gossypiella* (Saunders), the pink bollworms, but they also are evaluated on *Heliothis* spp. larvae. Even though many of these parasitoids were released, none was reported to have been recovered. After this series of shipments from India, the tachinid *Exorista segregata* Rond. was imported from Spain (1969) and the braconid *Bracon hebetor* Say (1973) and a *Trichogramma* sp. (1975) were imported from the USSR (Johnson et al. 1986).

Many of the species listed in Table 3 are currently being reared and studied. In Greece and Bulgaria, *Cotesia* (= *Apanteles*) *kazak* (Telenga) and *Hyposoter didymator* (Thunb.) were reported by Carl (1978) to be important parasitoids of *Heliothis armigera* Hübner. A biological control program in New Zealand was based on shipments of these two species from Europe, and *C. kazak* is now successfully established and extending its range in New Zealand. This wasp persists even in areas of insecticide use

Table 2. Parasitoids imported into the USA from India for biological control of Heliothis *spp.*

Species	Year(s) shipped	Destination states[1]
Hymenoptera: Braconidae		
Bracon brevicornis Wesmael	1954–55	NJ, IA, AZ, TX, NC, SC, TN, FL, MS
Apanteles angaleti Muesebeck	1954–55	NJ, AZ, TX, NC, SC, TN, FL, MS
Chelonus spp.	1954–57	NJ, AZ, TX, NC, SC, TN, FL, MS, HI
Microplitis indica Marsh	1964	GA
Hymenoptera: Ichneumonidae		
Enicospilus sp.	1964	GA
Campoletis chlorideae Uchida	1963–65 1967–68	AZ, GA, TX
Eriborus spp.	1964–65 1968	AZ, GA
Diptera: Tachinidae		
Palexorista laxa (Curran)	1963–65 1968	AZ, GA
Exorista xanthaspis (Wiedemann)	1964–65	GA
Carcelia spp.	1964–65 1967–68	AZ, GA
Goniophthalmus halli Mesnil	1966	NJ

[1]AZ = Arizona, FL = Florida, GA = Georgia, HI = Hawaii, IA = Indiana, MS = Mississippi, NC = North Carolina, NJ = New Jersey, SC = South Carolina TN = Tennessee, TX = Texas.

Table 3. Parasitoids imported into the USA for biological control of Heliothis *spp.*

Species	Origin	Year(s) shipped
Hymenoptera: Braconidae		
Cotesia kazak (Telenga)	Europe	1978, 1984
C. kazak	New Zealand*	1985
Microplitis demolitor Wilkinson	Australia	1981
M. rufiventris Kok	Egypt	1981, 1983
Hymenoptera: Ichneumonidae		
Hyposoter didymator (Thunb.)	Europe	1981, 1985
Heteropelma scaposum (Morley)	Australia	1981
Netelia sp.	Kenya	1982
Diptera: Tachinidae		
Palexorista laxa (Curran)	Kenya	1982

*Originally shipped from Europe to New Zealand.

and where the host density is low (Johnson et al. 1986). As a result of this success, arrangements were made for the shipment of *C. kazak* into the USA from Europe in 1984 and New Zealand in 1985.

Adults of the New Zealand strain lived nearly twice as long as adults of the European strain. Male (8.1 ± 0.8, n = 61) and female (11.4 ± 0.8, n = 50) *C. kazak* of European origin lived only half as long as males (14.9 ± 0.7, n = 65) and females (20.9 ± 0.7, n = 70) from New Zealand. The European strain may have become a "lab strain" after being reared in the laboratory for 19 months before the test was conducted. Specimens received from New Zealand, on the other hand, had been held in the laboratory for only 2 months before the comparison was made. Release of both strains against early-instar *Heliothis* spp. larvae in unsprayed cotton in Mississippi in 1985 yielded no recovery from collections of the target pest. However, releases of the New Zealand strain during 1986 resulted in recovery of this wasp from *H. zea* (Boddie) in cotton and from *H. virescens* (F.) in pigeonpea. This species may not compete well with our native *Cotesia marginiventris* (Cresson), or possibly the ecological conditions were to blame. Laboratory studies with *C. kazak* will include competition with native parasitoids, particularly *Microplitis croceipes* (Cresson). Results from these and other studies may indicate the likelihood of successful colonization in the field. According to Beirne (1975), initial colonizations may be favored by release of large numbers of parasitoids in semi-isolated release sites. Releases will include a complex of four or five species, with each species preferring different host sizes. The consequences of releasing laboratory-reared specimens is unknown.

Microplitis rufiventris Kok was colonized in our laboratory after being shipped from Egypt in 1983. Although this species is routinely reared on *Spodoptera exigua* (Hübner), field-cage studies were conducted in South Carolina to examine the potential of *M. rufiventris* against *Heliothis* spp. and *Pseudoplusia includens* (Walker). In greenhouse studies, *M. rufiventris* tended to prefer *S. exigua* over *P. includens* and *H. zea* on cotton plants (G.S. McCutcheon and W.W. Harrison, unpublished data).

Microplitis demolitor Wilkinson is one of the more common parasitoids that attacks *Heliothis* larvae in the field in Australia (Shepard et al. 1983). This species was imported in 1981 (Table 3), and is similar to our native *M. croceipes* (Cresson) in many respects. Both *M. croceipes* and *M. demolitor* significantly (P < 0.05) reduce feeding by *Heliothis* when the host is parasitized before reaching the fifth instar (J.E. Powell and G.G. Hartley, unpublished data). However, one behavioral difference is that larvae parasitized by *M. demolitor* remain on the foliage when the parasitoid pupates, whereas larvae parasitized by *M. croceipes* crawl down the plant and pupate in the soil. This characteristic might be important in a parasitoid sampling program.

In the USA, *M. demolitor* has been recovered practically everywhere that it has been released; for example, in sorghum in Arkansas, pigeonpea and soybean in South Carolina, soybean in North Carolina, and cotton in

Mississippi. This wasp has overwintered in field cages in South Carolina (J.F. Grant, unpublished data), and there is evidence that it may be established in North Carolina (K.E. Godfrey and K.G. Wilson, unpublished data). Field release of this species will be continued, in conjunction with release of *Palexorista laxa* (Curran), *C. kazak*, and *H. didymator.*

Hyposoter didymator was received in September 1985 from the U.S. Department of Agriculture European Parasite Laboratory in France, where it had been reared on the noctuid *Autographa gamma* for 4 months. So far, it has been reared successfully on *H. zea, H. virescens, P. includens*, and laboratory studies are being conducted to assess its biotic potential. *Hyposoter didymator* was released against *Heliothis* spp. in unsprayed cotton in Mississippi in 1986, but was not recovered.

The tachinid *P. laxa* from Kenya has been studied to a great extent in the laboratory. After releases in North Carolina, South Carolina, Mississippi, and Arkansas, small numbers were recovered in South Carolina and Mississippi. In the laboratory, this species often oviposits many times on a host larva; as the number of eggs deposited increases, the mean weight per puparium decreases. This results in size differential among adult flies. The relative number of progeny per medium and large female is significantly greater than that per small parent; thus, a rearing program would be aimed at producing a greater proportion of medium- to large-sized flies.

IMPORTATION PROGRAMS

Importation and establishment of new natural enemies entails a complex series of steps and a high level of coordination. Difficulties can arise at every phase, so researchers must be knowledgeable about potential problems and their solutions. The basic components of a program are exploration, importation, and release, but those perhaps most critical to receiving shipments safely are to *establish reliable contacts* at the natural enemy source and *arrange for maximum support* from the cooperating quarantine facility. Without these, failure is almost certain.

The principal steps involved in an importation effort are depicted in Figure 1. The four major phases of a project are: exploration, importation, field release, and evaluation. The groundwork is laid when the questions Who? What? When? Where? and How? are answered. Field-collected or laboratory-reared material will be shipped to a quarantine facility after all regulations are met. These are outlined in Jones et al. (1985). The logistics of getting a package from a source *to* a quarantine facility can be troublesome because (1) timing and safety are critical, and (2) changes between carriers increase the number of times a package is handled.

Once a shipment is secured by quarantine personnel, natural enemies
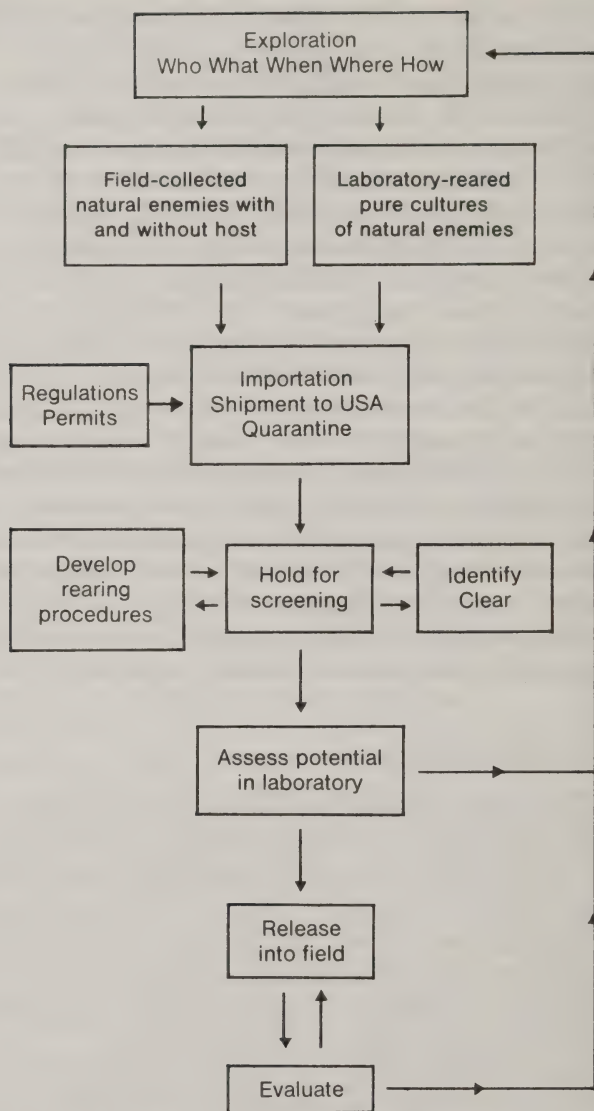
Figure 1. The principal steps in an importation program for natural enemies of pest species.

are screened for secondary parasitoids and reared, if possible, on the target host. Attempts to rear will be futile if the host is not accepted by the parasitoid, or if the environmental requirements for mating and oviposition are not met. Next, specimens are shipped to the U.S. Department of Agriculture Systematic Entomology Laboratory for identification; at times, however, specimens may be unidentifiable because (1) we lack

expertise for the particular group, (2) we lack reference specimens, (3) they represent a new species, or (4) the species is difficult to separate from other members of the group. This creates problems because an organism's release from quarantine security often hinges upon its identity. Meanwhile, laboratory tests can be conducted to assess the potential of the species in the USA. Studies might include host range, developmental biology, competition with native species, ecological requirements, and behavior.

A field release program will depend strongly upon our ability to rear the imported natural enemies, but releasing any number of specimens would be important. Simmonds (1976) stated that release of a beneficial species into a new area should not be delayed in order to find out more about its ecology, because introduction is the final test of the species capabilities. An evaluation program should be coupled with the release program in an attempt to monitor any progress. Evaluation of natural enemies is difficult and techniques are undefined, but such a program would include a sampling scheme, overwintering and diapause studies, observation of searching and dispersal behavior, and obtaining evidence of seasonal synchrony with host populations.

Intensive laboratory and field studies are being conducted on the braconid *M. croceipes*, a native of the USA. These studies include tolerance to insecticides and use of sex pheromone material to monitor wasp populations. Similar studies might yield important information on imported natural enemies.

Eight parasitoid species are currently being reared at Stoneville, and some also at other locations in the southern USA. They are the braconids *C. kazak, C. marginiventris* (Cresson), *Cardiochiles nigriceps* (Viereck), *M. rufiventris, M. demolitor,* and *M. croceipes*; the ichneumonid *H. didymator*, and the tachinid *P. laxa*. Specimens of certain species can be shipped to researchers who may be interested in using them in their own biocontrol programs. Those species listed for the USA are the more prevalent parasitoids found attacking *Heliothis zea* (Boddie) and *H. virescens* (F.) in the Delta of Mississippi.

Research requirements for a biocontrol program have been stated. Reliable contacts are essential for importing species from other countries. Support at quarantine facilities is excellent, and identifications are made expediently. Most of our parasitoids have adapted to our large-scale rearing methods, although none are mass-reared for augmentation efforts. The greatest need may be to define evaluation techniques. We must determine whether or not species previously released have become established in the field. For species not yet established, we should study ecological interactions with native natural enemies. This information may give us insight on improving the success of biological control.

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Importation and Establishment of New Natural Enemies of *Heliothis* into New Zealand

P.J. Cameron and *E.W. Valentine**

ABSTRACT

Heliothis armigera conferta (Walker) is the only member of the genus established in New Zealand. *H. punctigera* (Wallengren) is an occasional vagrant from Australia and probably does not form permanent breeding populations. Control of *Heliothis* has relied solely on chemicals until recent attempts to introduce parasites. Before these importations, the only parasite was a *Trichogrammatoidea* sp., which parasitizes eggs of several Noctuidae.

In 1968, one ichneumonid and three tachinids were imported from India but all failed to establish. Four *Trichogramma* spp. imported in 1974 from India also failed to establish. In 1976–77, *Hyposoter didymator* (Thunberg) and *Cotesia* (= *Apanteles*) *kazak* (Telenga) were imported from Europe. *H. didymator* was not released because of its wide host range, and because laboratory tests indicated it might interfere with the successful biological control of *Mythimna separata* (Walker). *C. kazak*, a specific parasite of *Heliothis*, was first released in 1977, recovered in 1981, and is now present in a large part of the northern half of the North Island.

A comparison of *H. armigera* populations before and after the establishment of *C. kazak* indicated that parasitism of small larvae was sufficient to alter the size distribution of larval populations. A study comparing larval populations at sites with and without naturally occurring *C. kazak* indicated that parasitism significantly reduced the proportion of larvae reaching damaging size, and reduced the consequent damage to tomatoes and soybeans. However, in crops with low damage tolerance, unacceptable losses occurred in the absence of chemical control.

In commercial tomato crops recolonization by *H. armigera* after insecticide treatment was accompanied by parasitism of small larvae. Permethrin appeared to have less effect on rates of parasitism than carbaryl. Future plans include further investigations with selective chemicals and *Bacillus thuringiensis* Berliner, wider distribution of *C. kazak*, and the importation of further parasites.

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Heliothis armigera (Hübner) is the only member of the genus established in New Zealand, and is referred to by Scott (1984) as the Pacific subspecies *conferta* (Walker). *H. punctigera* (Wallengren) is a sporadic summer vagrant from Australia and probably does not form permanent breeding populations. *H. armigera* is distributed throughout New Zealand but is more commonly reported as a pest in the North Island and northern areas of the South Island. Its food range is wide, principally the flowers and fruit of various legumes, the flowers of Compositae, and occasionally seedling Monterey Pine (Moore and Alma 1974). In cultivated crops it is most important as a pest of tomatoes, sweetcorn, beans, and seed lucerne, and is a minor pest on other vegetable crops and in home gardens.

In New Zealand, pupae of *H. armigera* diapause over winter and adults begin to emerge in September. There appear to be three overlapping generations producing a peak of flight activity in January and February (D.J. Allan, unpublished data). Larval infestations in crops are commonly first detected in January and persist into March and April, when pupae begin to enter diapause. Thus, periods with a high risk of infestation may be avoided by early planting.

Until recently control of *Heliothis* has relied solely on chemicals. This paper reviews the importation of parasites which has occurred since 1968. It considers the rationale behind the release of particular species and the selection of new candidate parasites. The impact of the newly established species, *Cotesia* (= *Apanteles*) *kazak* (Telenga), is described with reference to the possible development of integrated pest management (IPM) strategies.

PEST STATUS

Pest control of *H. armigera* is mainly directed against infestations on tomatoes. Crops for processing can receive up to seven insecticide applications at a total cost of $115/ha for chemicals, plus $116/ha for application costs (although insecticides and fungicides are usually applied together). This is one of several significant growing costs which total to $2913/ha (Anon. 1984). Pyrethroids are commonly used but no insecticide resistance to these or other chemicals has been reported. The development of such resistance in Australia (Goodyer et al. 1975; Gunning et al. 1984), and the threat of either transferral across the Tasman (Fox 1978) or local development of resistance, is a major reason for pursuing alternative control strategies.

A feature of New Zealand cropping which affects *Heliothis* is the lack of extensive and very frequently sprayed crops such as cotton and soybeans. Sweetcorn and green beans for processing each receive one regular

insecticide treatment, and other minor crops are treated as required. These cropping practices lower insecticide pressure sufficiently to reduce the probability of locally induced pesticide resistance.

When crops are not protected, considerable damage has been recorded. Tomatoes, in particular, are difficult to grow commercially without insecticides; for example, Jackson and Graham (1979) recorded 32% and Cameron and Valentine (1985) noted 38% damage in untreated crops. The incidence of *Heliothis* in corn is variable and sometimes *Mythimna separata* Walker may be mistaken for *H. armigera*. In adjacent blocks we have observed an apparent preference of *H. armigera* for tomatoes and soybeans, with no infestation of sweetcorn (Cameron and Valentine 1985). However, untreated sweetcorn can be severely damaged with up to 39% cob damage (Jackson and Graham 1979).

NOCTUID BIOLOGICAL CONTROL

Seven species of noctuids—namely *Agrotis ipsilon* (Hufnagel), *Chrysodeixis eriosoma* (Doubleday), *Mythimna separata* Walker, *Persectania aversa* (Walker), *Spodoptera litura* (F.), *Thysanoplusia orichalcea* (F.), and *H. armigera*—are regarded as being pests in New Zealand. With the exception of *P. aversa*, which is an endemic species, all are exotic, with established breeding populations, although *S. litura* is a regular immigrant from Australia and occasionally persists through the winter (Fox 1978). *T. orichalcea* is a very recent immigrant for which breeding populations were first discovered in the Auckland area in the summer of 1984–85 (M.G. Hill, unpublished data).

Two parasite species interact with a range of these species and directly or indirectly affect biological control of *H. armigera* (Table 1). *Trichogrammatoidea* sp., an indigenous parasite of eggs, was discovered by R.A.

Table 1. Host relationships of selected noctuid parasites

Egg parasites	Pest Noctuidae	Larval parasites
Copidosoma maculatum*	Agrotis ipsilon	
	Chrysodeixis eriosoma	
	Mythimna separata	Cotesia ruficrus*
	Persectania aversa	
Trichogrammatoidea sp.	Spodoptera litura	
	Thysanoplusia orichalcea	
	Heliothis armigera	Cotesia kazak*
	Graphania mutans	
	Other Lepidoptera families	

*Parasites imported into New Zealand.

Cumber (unpublished data) in 1974. He found that this unidentified species parasitized 60–100% of the eggs of *C. eriosoma* and *H. armigera* in tomatoes and recorded a wide host range in the laboratory.

The second parasite *Cotesia* (= *Apanteles*) *ruficrus* (Haliday), was introduced from Pakistan in 1971 to parasitize *A. ipsilon* (Cumber et al. 1977). Laboratory tests showed that *M. separata* was clearly an alternative target, and subsequent laboratory tests (Hill et al. 1985) have shown that *C. eriosoma* and the native noctuid *Graphania mutans* Walker are also suitable hosts. We have recently found that *C. ruficrus* consistently achieves 20–30% parasitism of *C. eriosoma* in field crops. However *M. separata* is the major host, frequently suffering 70–80% parasitism (Hill and Atkins 1983; Hill et al. 1985). The establishment of *C. ruficrus* is now considered to provide successful control of *M. separata* with considerable economic benefits. Estimates of these benefits range from NZ$4–10 million annually (Hill 1977; Mohyuddin and Shah 1977).

NEW IMPORTATIONS AGAINST *HELIOTHIS ARMIGERA*

None of the pest noctuids discussed above was considered to be controlled to an acceptable level by natural enemies before the program of importations was initiated in 1969 (Table 2). This program included specific *Heliothis* parasites as well as nonspecific parasites of noctuid eggs.

Larval Parasites, 1969

In 1969, four parasites of *Heliothis* larvae were imported from the Indian Station of the Commonwealth Institute of Biological Control (CIBC) at Bangalore: *Campoletis chlorideae* Uchida (Ichneumonidae) and three Tachinidae, *Eucelatoria armigera* (Coquillett), *Carcelia illota* (Curran), and *Palexorista laxa* (Curran). Where these parasites were imported under different names, the synonymy is given in Table 2. Cultures of all four species were established on *H. armigera* and the acceptability of some common noctuids was tested for *C. chlorideae* and *C. illota* (Hill et al. 1985). *C. illota* was found to develop on *C. eriosoma* but neither developed on *M separata*. Relatively few parasites of all species were released (80–650), and these releases were late in the season.

Egg Parasites, 1973

Four species of *Trichogramma* were introduced in 1973 from laboratory cultures maintained at the CIBC Station, Bangalore. The species were introduced as *T. australicum* Girault, *T. dendrolimi* Matsumura, *T. euproctidis* (Girault), and *T. evanescens* Westwood, and were considered to be general parasites of noctuid eggs. D.J. Allan (unpublished data) has

Table 2. Parasites *imported into New Zealand for control of* Heliothis armigera, *and the synonymy for species imported under other names*

Family Parasite (Synonymy)	Origin	Date	Status
Braconidae			
Cotesia kazak (Telenga) (= *Apanteles kazak* Telenga)	Europe	1977	Established
Hyposoter didymator (Thunberg)	Europe	1976	Not released
Ichneumonidae			
Campoletis chlorideae Uchida (= *Ecphoropsis perdistinctus* (Viereck))	India	1969	Not recovered
Tachinidae			
Eucelatoria armigera (Coquillett)	India	1969	Not recovered
Carcelia illota (Curran) (= *Eucelatoria illota* (Curran))	India	1969	Not recovered
Palexorista laxa (Curran) (= *Drino imberbis* (Wiedemann))	India	1969	Not recovered
Trichogrammatidae			
Trichogramma australicum Girault	India	1973	Not recovered
T. dendrolimi Matsumura	India	1973	Not recovered
T. euproctidis (Girault)	India	1973	Not recovered
T. evanescens Westwood	India	1973	Not recovered

recorded the rearing, release, and limited survey results. All *Trichogramma* species were successfully cultured on the eggs of *M. separata, A. ipsilon, G. mutans, Ctenoplusia albostriata* Bremer & Gray, and *Galleria mellonella* (L.), as well as the main target species *H. armigera* and *C. eriosoma.* Many thousands of all four species of *Trichogramma* were released in 1974 and 1975 in the Auckland area and in Rarotonga, Cook Islands.

Surveys, 1974–1976

Surveys carried out from 1974 to 1976 included the sampling and rearing of noctuid larvae and eggs from a range of crops throughout the release areas for *Heliothis* parasites. No imported species were recovered. However, *Trichogrammatoidea* sp. was confirmed as a significant parasite of noctuids, parasitizing 89% of *Heliothis* eggs in more northern areas (R.L. Hill, unpublished data).

Larval Parasites, 1976–1977

Since no parasites of *Heliothis* larvae are known in New Zealand

(Valentine 1967), further searches were undertaken in southern Europe by the European station of CIBC in 1975–76 (Carl 1977). Two species reared from field-collected *H. armigera* were selected as promising parasitoids for shipment to New Zealand (Carl 1978). *Hyposoter didymator* (Thunberg) (Ichneumonidae) was received in 1976 and *Cotesia kazak* (Telenga) (Braconidae) in 1977. Most *C. kazak* for shipment were reared on *Heliothis virescens* (F.). Routine host preference tests in New Zealand (Hill et al. 1985) showed that *C. kazak* was specific to *Heliothis*, but *H. didymator* had a wide host range. Of 24 lepidopteran species presented to *H. didymator*, 20 were stung and the parasite developed successfully on 14 species from four families. All the noctuids in Table 1 were hosts. Two of the suitable non-noctuid hosts, *Epiphyas postvittana* (Walker) (Tortricidae) and *Pseudocoremia rudisata* (Walker) (Geometridae), are likely to be encountered in the field by *H. didymator*, and they were also readily accepted in comparative tests. These results caused concern for the possible impact of this polyphagous parasite on indigenous species.

Further laboratory trials by Hill et al. (1985) examined the impact of *H. didymator* on the relationship between *C. ruficrus* and *M. separata* and the effect this might have on control of this noctuid. *H. didymator* usually out-competed *C. ruficrus* in the same larva. Hill concluded that "possible interference with the *M. separata*/*C. ruficrus* host/parasitoid relationship precluded its release for *H. armigera* control. . . . The biological control of *M. separata* by *A. ruficrus* was valued at $4 million in 1976 (Hill 1977), and even minor perturbation of this stable relationship could cause economic losses." The decision not to proceed with investigations on *H. didymator* reflected both the difficulty of obtaining and evaluating further biological information on this species and the availability of an alternative specific *Heliothis* parasite, *C. kazak*. Subsequent efforts were therefore concentrated on the rearing and release of *C. kazak*, and no *H. didymator* were released.

Release and Dispersal of *C. kazak*

C. kazak was successfully reared on *H. armigera* (Singh et al. 1982) and first released in 1978 (Hill et al. 1985). Further extensive releases were made at 27 sites in northern regions of the North Island (Figure 1) in the summer of 1979–80 (E.P. Burgess, personal communication). Releases consisted of parasitized caterpillars, cocoons, and adults at the rate of approximately 60 individuals per site. The majority of sites were maize crops or weedy roadside areas containing *Lotus pedunculatus*.

The first field recovery of *C. kazak* was a single specimen from several *H. armigera* larvae collected on an ornamental *Cleome* sp. (Papilionaceae) in March 1981, in the gardens of the Mt. Albert Research Centre in
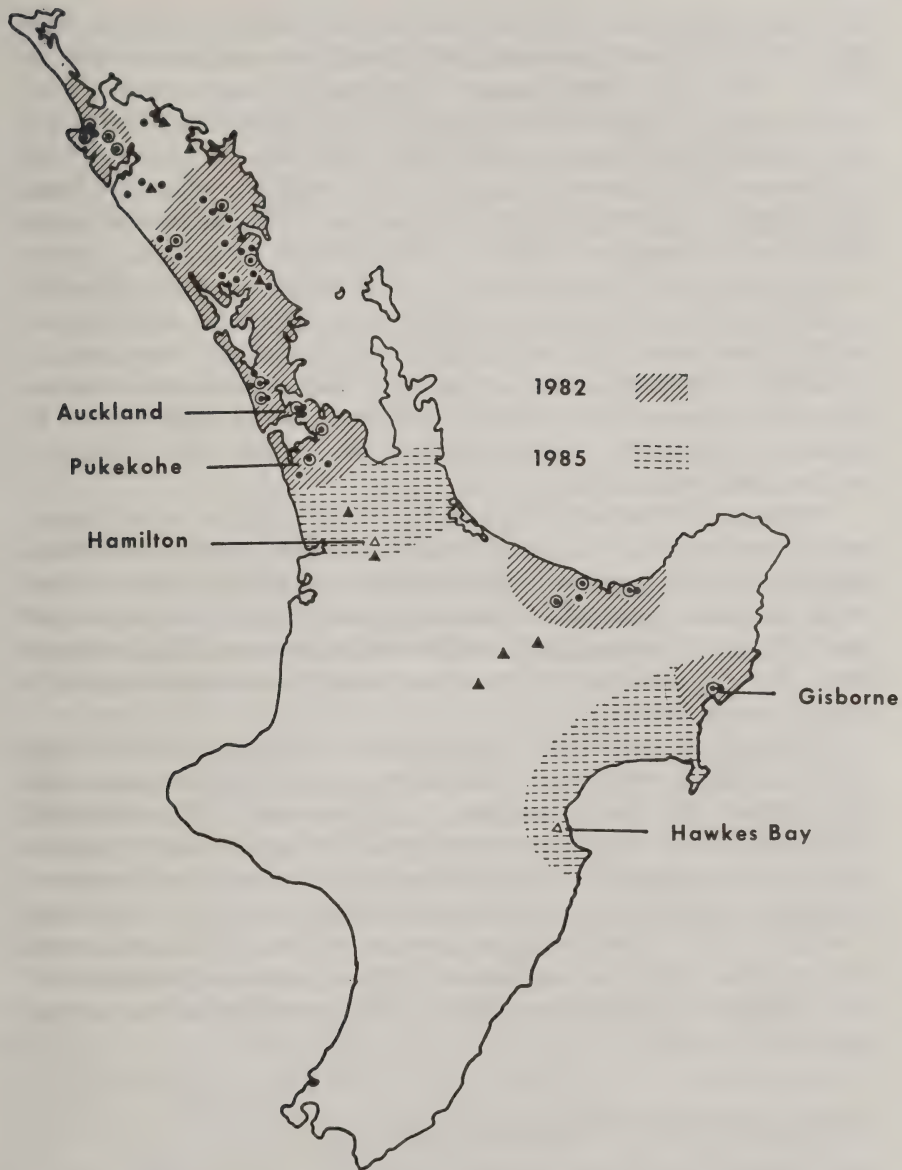
Figure 1. Release and recovery sites for *Cotesia kazak*, 1977–1985. ● = release site 1979–80, ⊙ = recovery site 1982. ▲ = nil recovery 1982, △ = recovery site after 1982. Probable areas of establishment for 1982 shown by cross-hatching, and for 1985 by dashes.

Auckland, 11 months after the last release. Further recoveries were obtained from the same site early in 1982 and from a soybean crop at the DSIR Pukekohe Research Station, 40 km south. This prompted a more extensive survey centered on the release sites. *C. kazak* was recovered in the vicinity of most release areas (Figure 1) and was found up to 10 km from release sites. Extensive sampling of *H. armigera* in vegetables, roadside weeds, and lucerne defined a distribution in 1982 which was largely determined by the pattern of releases in warmer and coastal areas. Approximately a year later, in March 1983, *C. kazak* was found to have dispersed southwards to Hamilton, at least 60 km from the nearest previously known establishment site at Pukekohe. In the intervening period, the presence of *C. kazak* at Pukekohe and its absence from Hamilton allowed an assessment of the impact of the parasite. The known natural distribution of *C. kazak* by March 1985 included Hawkes Bay, about 100 km south of previous recoveries in 1983.

Although *C. kazak* appears to be dispersing rapidly by natural means, we have now begun active distribution of the species. Shipments have been made to northern areas of the South Island for release in lucerne seed crops. Nucleus cultures have also been supplied to the U.S. Department of Agriculture in Mississippi, at Stoneville; the Department of Agriculture in Perth, Western Australia; and the Plant Protection Research Institute in Pretoria, South Africa.

Hyperparasitism of *C. kazak* cocoons is not regarded as being significant in cultivated areas. The only record of a hyperparasite is of a single species of *Trichomalopsis* (= *Eupteromalus*) (Pteromalidae), which may have resulted from chance parasitism targeted at a *Glyptapanteles* sp. parasitizing tortricid caterpillars on a noncrop plant. No secondary parasites have been reared from *C. kazak* cocoons from crop plants. The high levels of hyperparasitism reported by Carl (1977) from Europe have not been detected in New Zealand. The low incidence of hyperparasitism is probably an important factor in the successful establishment and spread of *C. kazak*.

EVALUATION OF *COTESIA KAZAK*

The establishment of *C. kazak* as the only larval parasite of *H. armigera* provided the opportunity to examine its impact by comparing larval populations before and after establishment and in areas with or without the parasite. This evaluation is described in Cameron and Valentine (1985). Only small larvae are parasitized, and from field collections no larvae larger than 10 mm produce parasites. The first comparison relied on baseline data which recorded larval size distribution for unparasitized *H. armigera* in soybeans (Cameron et al. 1986).

Table 3. Comparison of size distribution (% in each size category) of Heliothis armigera *larvae with and without parasitism by* Cotesia kazak *(adapted from Cameron and Valentine 1985)*

Size category (mm)	Establishment comparison		Site comparison	
	1981 Before	1982 After	1983 No parasite	Parasite
1–5	9.8	21.8	6	20
6–10	25.5	61.8	29	34
11–15	23.5	5.5	25	22
16–20	21.6	4.6	20	12
>20	21.6	7.3	20	12
n	51	55	345	441
% parasitism of larvae ≤10 mm long	0	52	0	45

Substantially fewer larvae appeared to reach the larger size categories in 1982, when parasitism over the season averaged 52% (based on larvae less than 10 mm long) (Table 3). The subsequent comparison between Pukekohe (with parasites) and Hamilton (without parasites) was carried out early in 1983, while *C. kazak* retained its 1982 distribution (Figure 1). A designed comparison of larvae (on tomatoes and soybeans) over eight weekly sampling occasions confirmed that *C. kazak* reduced the proportion of larvae reaching damaging size (Table 3). Other factors contributing to differences in larval size distribution between sites were minor compared with the 45% parasitism (Cameron and Valentine 1985). This level of parasitism compensated for greater larval recruitment at Pukekohe, and resulted in significantly fewer larvae reaching the large categories than at Hamilton, where there were no parasites (Figure 2).

Crop damage was also significantly less where *C. kazak* was present (Table 4), although it was apparent that the proportion of fruit damaged in tomatoes was still unacceptable. Our experiments, and those of Room (1983) and Burkett el al. (1983) for *H. zea*, suggest that *H. armigera* larvae do not move significantly on tomato plants until they reach third instar or are greater than 10 mm in length. Location of fruit and subsequent damage was greater with larvae greater than 15 mm in length. The benefits we have measured from the establishment of *C. kazak* appear to be a result of this selective mortality of small larvae, rather than any observable effects on general population levels.

PROSPECTS FOR IPM

Carl (1978) noted the persistence of *C. kazak* in areas of southern Europe

	Larval size category (mm)				
	1	2	3	4	5
		(<10)			(>20)
Sampling occasion (weeks)					
1	+	−	−	.	.
2	.	−	+	.	+
3	−	−	−	+	+
4	**+**	+	−	−	−
5	**+**	+	−	−	**−**
6	**+**	.	−	−	**−**
7	**+**	+	+	−	**−**
8	−	+	−	−	+

Figure 2. Comparison of the proportion of larvae in each size category between sites with and without *Cotesia kazak*. Negative signs indicate fewer larvae at Pukekohe (with parasites) than at Hamilton (without parasites), positive signs indicate the reverse, and a dot is equality. Bold signs indicate significant differences. Adapted from Cameron and Valentine (1985).

Table 4. Comparison of percent fruit damage by Heliothis armigera *at sites with and without* Cotesia kazak *(adapted from Cameron and Valentine 1985)*

Crop	Hamilton (without parasite)	Pukekohe (with parasite)	Comparison (ANOVA)
Tomatoes	37.8	29.7	$P < 0.05$
Soybeans	7.9	4.8	$P < 0.05$

where insecticide usage was common. We have similarly found *C. kazak* in commercial crops in New Zealand. In crops where longer spraying intervals have allowed recolonization by *H. armigera*, the small larvae were often parasitized. In a preliminary trial we compared the rate of reinvasion in tomatoes treated with carbaryl, permethrin, or no insecticide. As the insecticidal protection declined 3 to 4 weeks after treatment, parasitism appeared to be greater in the permethrin and untreated plots (Figure 3). This suggests that with either deliberately or unintentionally longer treatment intervals, particular chemicals may selectively favor parasites. The optimization of treatment intervals and the selection of chemicals or biocides such as *Bacillus thuringiensis* Berliner will be the subject of future investigations.
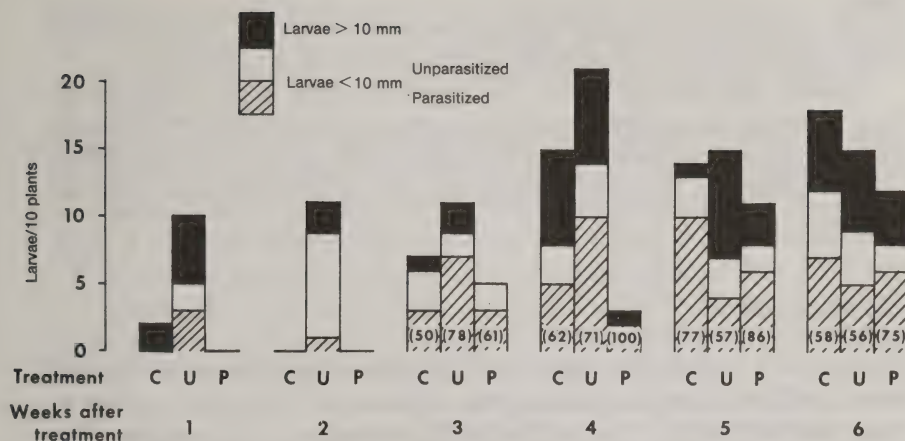
Figure 3. Reinvasion of tomatoes by *Heliothis armigera* in plots treated with carbaryl (C), permethrin (P) (both at recommended rates on 23 Feb. 1984) or untreated (U). Solid black represents larvae >10 mm and the remainder is larvae ≤10 mm. Cross-hatching indicates parasitism, and the number in parentheses is the percent of small larvae parasitized. There are significant treatment differences (ANOVA, P < 0.05, n = 10) for total larvae up to 4 weeks after treatment.

The establishment of *C. kazak* is likely to make a significant contribution to control of *H. armigera* in unsprayed field crops, vegetables, or weedy areas which serve as reservoirs. In crops such as soybeans, with higher damage thresholds, increased parasitism will be of benefit. However, present natural controls do not sufficiently reduce damage in crops with low damage thresholds. In New Zealand 10% total damage from all sources is acceptable without penalty in tomato crops for precessing (J. Wattie Cannery, pers. comm.). Such high levels of control have not been reported in programs based on larval parasites alone, but there may still be scope in New Zealand for increasing larval parasitism early in the season, between insecticide treatments, or in reservoir areas.

Present levels of parasitism by *C. kazak* in 1985 averaged 48–83% for *H. armigera* larvae from beans, tomatoes, and lucerne at various stages of the growing season. In tomatoes, both *H. armigera* infestations and parasitism continue to increase almost to harvest. As earlier planting is recommended to avoid the late-season buildup of *H. armigera*, the activity of *C. kazak* in early crops should be investigated. If *C. kazak* is not effective in early crops it may be necessary to introduce different parasites. Larvae which at present escape parasitism by *C. kazak* and grow larger than approximately 10 mm are not attacked by any parasites. A possible further parasite which is likely to complement the host size preference of *C. kazak* is *Microplitis croceipes* (Cresson). Powell and King (1984), using methods comparable to those of Cameron and Valentine (1985), show that this

North American species prefers *H. zea* larvae which are predominantly 10 to 25 mm. We plan to import this parasite to attack *H. armigera*.

Finally, the possible role of *Trichogramma* spp. for introduction by inoculative or inundative release should be considered. The present scale of cropping in New Zealand may not warrant the resources for inundative release programs, but introduction and natural colonization would be feasible.

CONCLUSION

The recovery and establishment of *C. kazak* several years after its final release indicates that this parasite may have required a period to adapt to New Zealand conditions or to the Pacific subspecies of *H. armigera*. The pattern of recovery suggests that there were many successful establishment sites and that increases to detectable numbers took approximately 2 years. The continuing natural spread of the parasite should ensure that it reaches all susceptible crops within major geographic areas, and artificial distribution is planned only between major areas. Rates of parasitism are high and may still be increasing.

Although *C. kazak* has been identified as a significant component for future IPM programs, alone it provides insufficient control in crops with low damage thresholds. The use of synthetic pyrethroids at optimum application intervals may minimize damage and allow *C. kazak* to provide some protection against reinvasion. In the longer term, the probability of resistance to synthetic pyrethroids may favor the use of selective insecticides together with parasites. In New Zealand, where only one larval parasite is present, the establishment of further parasite species is proposed.

Acknowledgments

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Increasing the Effectiveness of Natural Enemies for the Suppression of *Heliothis* Populations

Introduction

D.J. Greathead and *D.N. Srivastava**

Natural enemies of *Heliothis* spp. are numerous, and research has shown that they are capable of contributing substantial rates of mortality. However, the contribution of native and introduced natural enemies is inadequate to suppress *Heliothis* spp. populations to a level that provides adequate crop protection. Natural enemies usually build up too late or are insufficiently active in the target crops to prevent damaging outbreaks. Therefore, this session explores research into means of manipulating natural enemies to enhance their impact.

First, experience in the Western Hemisphere in attempting to augment natural enemy action by timely release of laboratory-reared parasitoids and predators is examined. Here, attention is drawn to the importance of developing reliable techniques to ensure the production of enough insects and their release in sufficient quantities at the right time to achieve the desired effect. The possibilities for improving performance by the development of more effective strains are also explored. This is complemented by a review of attempts to augment natural enemies in India, which draws attention to the importance of the technical problems already highlighted.

Behavior-modifying chemicals have been the subject of recent research and we are beginning to understand their role in controlling insect behavior but do not yet have sufficient knowledge of behavior mechanisms in nature to apply the chemicals effectively. The third paper provides a guide to present understanding and the research needed to make behavior modification an effective tool in pest management.

Insect pathogens are potentially valuable pest control agents for use as selective insecticides. Experience in the USA has shown the feasibility of using virus preparations on an experimental scale but the commercial exploitation of viruses has proved difficult. Again, the potential benefits and problems of large-scale use are emphasized from experience in India.

The final paper provides a stimulating look into the future and shows how genetic engineering is on the brink of solving some of the problems of commercialization and enabling the creation of new and more effective products.

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Thus there is potential for the manipulation of parasitoids, predators, and pathogens by conventional means, as well as exciting new possibilities arising from basic research. To achieve this potential, much more careful quantitative research is required to establish reliable techniques for the production and effective application of natural enemies on a large scale as a major component of *Heliothis* pest management.

Control of *Heliothis* spp. (Lep.: Noctuidae) in the Western Hemisphere by Propagation and Release of Predators and Parasites, Including the Use of Genetically Improved Strains

E.G. King*, *J.E. Powell**, and *W.M.M. Steiner***

ABSTRACT

Research efforts needed to advance predator and parasite augmentation as a management strategy (or integrated approach component) for *Heliothis* spp. are discussed. Genetic improvement of entomophagous arthropods through genomic modification or selection techniques for specific attributes holds promise for greatly increasing the effectiveness of augmentation, either as a result of improved field performance or indirectly from reduced rearing costs. Research efforts must be directed at measuring parameters influencing the field efficacy of laboratory-reared entomophages and the development of methodology for sustained, efficient mass propagation of high-quality organisms, *in vivo* and eventually, *in vitro*.

INTRODUCTION

Any effort that results in an increased predator or parasite density may be considered biological control by augmentation. Such an increase in natural enemy numbers may be achieved by: (1) providing supplementary food; (2) applying behavior-modifying chemicals; (3) capture and redistribution; or (4) propagation and release. The scope of this article will be restricted to elements of propagation and periodic release of predaceous and parasitic arthropods (entomophages) of *Heliothis*.

The goal of biological control by augmentation should be suppression of *Heliothis* and its damage to acceptable levels. This goal will most likely
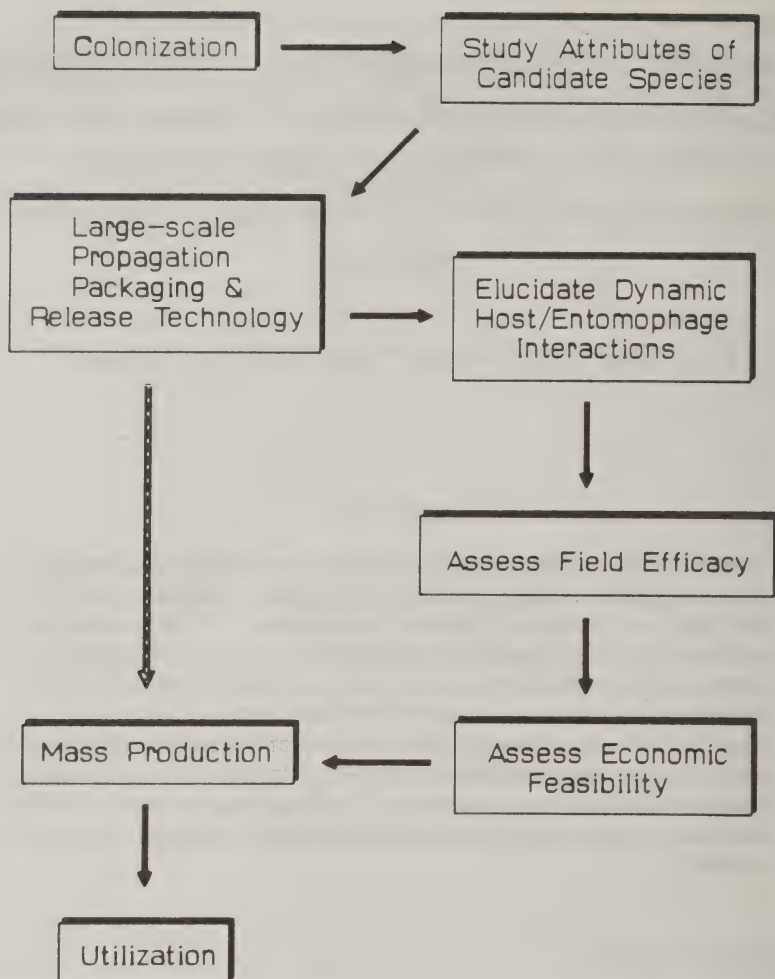
Figure 1. Biological control of *Heliothis* by propagation and release of predators and parasites.

be attained in concert with other pest management tactics. Depending on the entomophage used, the effective management unit selected for an augmentation program could be a single field, a geographically defined plant community, or an entire agroecosystem. The flow of events for a propagation and release program, with solid lines representing research and development pathways critical to goal achievement, is shown in Figure 1. Ideally, each event should be completed before proceeding to the next one, except for those which may be researched as a parallel activity, here signified by a broken line.

Summarizing data from individual states in the southern USA, Goodenough et al. (1986) listed the periods of activity of key entomophages against *Heliothis*. Butler et al. (1982) and van den Bosch and Hagen (1966) have compiled information on important natural enemies of *Heliothis* for other regions in the USA.

An initial step in an augmentation program is the colonization of those predators and parasites showing potential for regulating *Heliothis* populations. Colonies established from field collections of natural enemies generally have supplied researchers with sufficient numbers of organisms to enable bionomic studies. Colonization of these natural enemies has been facilitated by the development of small-scale rearing procedures and artificial diets for *Heliothis* (Raulston and King 1984). Parasites and predators have been reared to study instar preferences and estimate search rates to assess the feasibility of augmenting their numbers. Numerous species have been evaluated for their potential as biocontrol agents in a propagation and release program. Three organisms will be emphasized in this paper: (1) the braconid *Microplitis croceipes* (Cresson); (2) the egg parasite *Trichogramma pretiosum* Riley; and (3) the predator *Chrysopa carnea* Stephens. Each organism is now being researched in the USA, and all are potential candidates for propagation and release programs.

ATTRIBUTES OF CANDIDATE SPECIES

High search-rate capability, host/prey specificity, high power of increase, and adaptability to the abiotic environment have been mentioned as the main attributes of a density-responsive biological control agent that successfully regulates a host/prey population (Huffaker et al. 1976; Carl, K.P., these Proceedings). While life cycle synchrony and a high intrinsic rate of increase of the entomophage relative to that of its host/prey are certainly desirable, periodic augmentative releases may obviate the need for a particular entomophage to exhibit these attributes. Biological control of a multivoltine pest such as *Heliothis*, with its large reproductive capacity and high mobility, may be best accomplished by augmentation. Thus, a candidate parasite or predator for an augmentation program may exhibit a limited complement of attributes and still be effective in suppressing a *Heliothis* population. In determining how and when to use an entomophage for biological control, it is important to establish the reasons for which a particular entomophage is unable to naturally suppress *Heliothis* to acceptable population levels. Regardless, high survivorship under field conditions and efficiency in discovering and attacking *Heliothis* is required. Ideally, the released entomophage should be capable of successful reproduction with subsequent generations contributing to the regulation of *Heliothis* populations. In addition, because *Heliothis* is usually part

of a pest complex attacking a crop, pesticide tolerance by an entomophage is desirable, and may be necessary for augmentation to be operationally feasible.

GENETIC IMPROVEMENT

Genetic improvement of a candidate entomophage through classical selection techniques or genome modification has great promise for dramatically increasing the effectiveness of augmentation. Reduced rearing costs and/or improved field performance may result from these measures. In essence, the entomophage becomes endowed with an attribute or characteristic not previously possessed or only weakly expressed. Before attempting genetic improvement of an entomophage, one must identify the desired attributes and determine if they are amenable to genetic improvement. For a particular attribute, the existence of sufficient natural variation may be limited, and collection of various biotypes may be required to establish the bounds of genetic variability. Genetic variation is important because it may correlate with ease of genetic manipulation, and the identification of genetic markers facilitates the study of gene organization, gene mapping, and population movements.

Fitness components (fecundity, sex ratio, etc.) associated with each attribute must then be identified; the interaction of fitness components may be established by using classical selection procedures. Failure to recognize all fitness components affecting a particular attribute one wishes to modify may result in failure of the genetic improvement program due to pleiotropic effects of genes related to the fitness components. Fitness-related interactions depend on epistatic and pleiotropic effects of genes. Therefore, any approach intended to genetically improve an entomophage will be aimed at maximizing fitness without sacrificing other traits or attributes.

Genetic evidence for control of a particular fitness component, i.e., simple or polygenic inheritance, must be demonstrated. A genome may possibly be modified for fitness components controlled by one (or a major) gene, however, enhancement of components that are polygenically controlled will probably be limited to use of classical selection programs due to present limitations on the amount of transferable genetic material between individuals.

Selection for or genetic modification of biotypes having improved biological characteristics, such as higher fecundity, female-biased or uniparental sex ratio, and more rapid developmental periods, could greatly reduce rearing costs of natural enemies (Roush 1979). For example, Urquijo (1951) was able to improve the searching ability of *T. minutum*

Table 1. Allozyme frequencies in a laboratory colony of Microplitis cro-
ceipes established from a Georgia cotton field collection[a]

Locus	Number analyzed	Allele			X²HW
		4	5	6	
Pgi-1	114	—	0.719	0.281	**
Got-1	47	—	0.841	0.159	ns
6-pgdh	28	0.089	0.911	—	ns
Est-2	55	—	0.773	0.227	ns
Est-4	27	0.037	0.963	—	ns

**Hardy-Weinberg X² is 9.91, P > 0.99 with 2 df.
ⁿˢHardy-Weinberg equilibrium prevails.
[a]W.M.M. Steiner, unpublished data.

Riley, and Orphanides and Gonzales (1970) successfully colonized a uni-
parental strain of *T. semifumatum.*

A nondiapausing, carbaryl- and organophosphorus-resistant strain of
Metaseiulus occidentalis (Nesbitt) has been selected and evaluated for
biological control of spider mites on roses (Field and Hoy 1986). Powell et
al. (1986) found that *M. croceipes* was relatively tolerant of pyrethroid
compounds and that its response was highly heterozygous. In fact, genetic
variation in the form of isozyme systems have been found in this parasite
(Table 1). Thus, the distinct possibility exists that a genetically improved
biotype of this species, highly tolerant of pyrethroids, yet retaining those
attributes essential for effective suppression of *Heliothis*, could be
produced.

The problem of extreme susceptibility of *Trichogramma* spp. to most
pesticides might conceivably be minimized through selection of a labora-
tory strain for increased tolerance and/or resistance to a pesticide(s). Kot
et al. (1975) attempted to induce resistance to DDT and demeton-S-methyl
in five different populations of *T. evanescens* Westwood. However, they
were unable to establish a strain that was genetically stable and concluded
that either the recessive character for resistance or the inadequacy of the
selection method was responsible.

LARGE-SCALE PROPAGATION, PACKAGING, AND RELEASE
TECHNOLOGY

After selection of a candidate species, further evaluation is severely limited
without technology for large-scale propagation, packaging, and distribu-
tion of the parasites. *Microplitis croceipes*, a solitary larval parasitoid
selective for *Heliothis*, is one of the most prevalent and perhaps most
important larval parasites attacking *Heliothis* in the southern USA (King

et al. 1985d). This wasp possesses many of the attributes previously mentioned, is relatively tolerant of certain insecticides presently used for insect control in cotton, and is particularly tolerant of the pyrethroids (Powell et al. 1986).

Large-scale rearing of *M. croceipes* is accomplished by exposing several hundred *H. virescens* (F.) larvae in fiberglass trays to caged parasites for a designated time (Powell and Hartley 1987). A 903-cell polystyrene insert fits into the tray containing a soybean flour-wheat germ diet (King and Hartley 1985). The cells provide spatial separation to prevent larval cannibalism. After larvae are exposed to the adult parasites, a porous polypropylene sheet is secured atop the cell insert. Upon emergence from their moribund hosts, the parasite larvae spin cocoons on the polypropylene sheet and upper portions of the cell insert. Parasite cocoons are easily harvested using a sodium hypochlorite (0.4%) wash; subsequent isopropyl alcohol (70%) wash separates cocoons from host larval exuviae.

The success of this rearing program may be attributed to the following factors: (1) a continuous host supply; (2) capability of regulating developmental rates of host and parasites; (3) appropriate environmental conditions; (4) sanitary rearing conditions; (5) means of suppressing microbial contaminants and disease epizootics; (6) adequate space, supplies, equipment, and support; and (7) multicellular host rearing techniques (Powell and Hartley 1987). This large-scale rearing procedure has permitted research on biotype selection and genetic improvement, pheromone isolation and identification, movement of the parasite relative to *Heliothis* density, toxicological studies, and modeling of host/parasite population dynamics. These research areas constitute critical events in the development of an augmentation program.

Rearing of *C. carnea* larvae is accomplished by isolating eggs of this species in multicellular rearing units that are covered on both sides with organdy fabric (Morrison and King 1977). Upon hatching, larvae feed through the fabric screen on a honey-water 1:1 mixture layered on a glass plate. After pupation, the fabric screen is removed and adults are allowed to emerge from cocoons in containers provided with diet and oviposition substrate. Eggs are harvested from the substrate and may be recycled into the colony or used in field releases. Eggs destined for field distribution are prepared by mixing with sawdust and frozen *Sitotroga cerealella* (Olivier) eggs. When 2–3 days old, larvae are dispensed in the sawdust medium from a backpack- or tractor-mounted distribution unit (Jones and Ridgway 1976).

Probably the best known example of an entomophage in the Western Hemisphere that has been mass produced and distributed for augmentative releases to control *Heliothis* is *T. pretiosum*. Other species within this genus are employed for *Heliothis* suppression in the Soviet Union, Peo-

ple's Republic of China, and perhaps to a greater degree in Latin America (King et al. 1985a).

ELUCIDATION OF DYNAMIC *HELIOTHIS*/ENTOMOPHAGE INTERACTIONS

Hopper and King (1984) reported that *H. virescens* larvae parasitized by *M. croceipes* move and feed less on cotton than unparasitized larvae. With this parasite, we are well into the process of elucidating dynamic host-parasite interactions. Actual use of this parasite in an augmentation program for biological control of *Heliothis* depends on its suppressive capability and the economics of production and release. Expanded field evaluations are being conducted.

Field Efficacy

Release of about 17,000 *M. croceipes* adults in a small cotton field resulted in 76% parasitization of *Heliothis* larvae; 95% of fifth-instar larvae were parasitized by a complex of larval parasites (K.R. Hopper, J.E. Powell, and E.G. King, unpublished data).

Various researchers have demonstrated that *C. carnea* larvae can suppress *Heliothis* larvae when released in sufficient numbers (Lingren et al. 1968; Ridgway and Jones 1968). Ridgway and Jones (1969) concluded that 123,500 *C. carnea* second-instar larvae per hectare could provide effective control of *Heliothis*.

The technical feasibility of augmenting *T. pretiosum* populations to reduce damage to tomato has been reported by Oatman and Platner (1978). However, the presence of other Lepidoptera (*Spodoptera*) not attacked by this parasite complicated field evaluation. *Heliothis* egg parasitism in cotton has generally increased greatly after field releases of *T. pretiosum* (Stinner et al. 1974; Ables et al. 1979).

Ridgway et al. (1981) and King et al. (1984) have identified several factors that limit use of *Trichogramma* for control of *Heliothis* in the USA. Possible explanations for erratic results are:

1. Incomplete knowledge of the population dynamics of *Heliothis* and imprecise quantitative survey methods hamper efforts to accurately predict onset, intensity, and duration of *Heliothis* oviposition.

2. Insufficient knowledge to predict *Heliothis* egg mortality for dynamic host egg and *Trichogramma* densities; decisions on *Trichogramma* release intervals and rates must be based on predictable larval densities as impacted by released parasites in addition to other mortality factors.

3. Poor fitness of released *Trichogramma*.

Assessing Economic Feasibility

Chrysopa carnea costs of $12.50 per 4000 predator larvae (E.J. Dietrick, Rincon Vitova, pers. comm.), indicate that this approach is not economically feasible in the USA when compared with alternative control measures (King et al. 1985c).

A 31% yield reduction was reported (King et al. 1985b) in untreated checks compared with *Trichogramma* release fields in North Carolina. However, a 23% yield reduction in release fields compared with insecticide-treated fields was reported in this same area. Consequently, when revenue net of control costs was calculated, the insecticidal control method was most profitable. Thus, the costs and effects of alternative control measures must be considered when assessing economic feasibility of an augmentation program.

MASS-PRODUCTION TECHNOLOGY

Inability to efficiently mass-produce predators and parasites of consistently high quality is a major factor limiting commercialization of the augmentation approach in the USA. Development of artificial diets and *in vitro* rearing techniques may minimize production costs and assure adequate nutritional qualities to produce suitable predators and parasites. Artificial diets have been developed for rearing several natural enemies (Greany 1986), and *in vitro* rearing systems have been developed for *Trichogramma* and *Eucelatoria* (Hoffman et al. 1975; Nettles et al. 1980).

Trichogramma spp. are the only arthropods presently being mass-produced and released for biological control of *Heliothis* in the Western Hemisphere. Other parasites and predators are being mass-produced for control of other pests, particularly of citrus.

CONCLUSIONS

Unless field effectiveness can be maintained, laboratory selection of biotypes with desirable attributes will have little impact in an augmentation program. Field data will be needed to document the practical benefits of selective breeding/genetic modification of natural enemies released to suppress *Heliothis*. For example, just as it is deemed necessary to establish basic ecological factors optimal for entomophage activity, it may also be necessary to establish those genetic or internal environmental factors which optimize entomophage activity and efficiency. Given the heavy use of insecticides in the USA and other countries, it seems appropriate to suggest that understanding the genetics of insecticide resistance in parasites and predators offers a clear target on which to concentrate research

effort. Development of insecticide-resistant strains would clearly benefit any augmentation program.

Development of the capability to mass propagate entomophagous arthropods (*in vivo* or *in vitro*) must be considered an essential research event before the use of predators and parasites to suppress *Heliothis* becomes economically feasible. Present mass-propagation efforts should be expanded with emphasis on improving the efficiency and economics of production, particularly those entomophages for which *in vitro* rearing appears probable. Advancement in *in vitro* rearing capability should result from further research in isolating and identifying kairomones mediating oviposition, defining endocrinological and nutritional requirements, determining optimum environmental ambients for growth, formulating and packaging, developmental media, and integrating the various components to produce entomophages by *in vitro* production.

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Control of *Heliothis* Species (Lep.: Noctuidae) by Augmentative Releases of Predators and Parasites in India

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ABSTRACT

There has been no commercial use of parasites and predators against *Heliothis* spp. in India, although there have been several augmentation trials against *Heliothis armigera* (Hübner), mainly on cotton and tomato, but also on other crops. Some of these trials have tested inoculative releases of native and exotic larval parasites with some success, but many have tested inundative releases of native and exotic *Trichogramma* spp. Most of the inundative release trials have been on small unreplicated plots, with no attempt to measure the economic benefit. It is suggested that research should now be concentrated upon the economic evaluation of augmentation in the most promising situations, so that the potential for biocontrol in the management of *Heliothis* spp. can be determined. The related areas of research priority are also discussed.

The value of entomophaga for regulating and controlling agricultural pests has long been recognized. In ancient times, Chinese farmers placed nests of the predatory ant, *Oecophila smaragdina* (F.), in citrus trees to control various leaf-eating insect pests (Doutt 1964). Importation of exotic natural enemies (classical biocontrol) also showed spectacular success in pest control nearly a century ago (Caltagrione 1981). However, conscious manipulation and utilization of arthropods was all but abandoned by most entomologists with the advent of modern pesticides in the 1940s (Rabb 1970). Subsequent concern over the misuse or overuse of pesticides has resulted in renewed interest in biocontrol as an important component of pest management. A recent survey on the utilization of the egg parasites, *Trichogramma* spp., during 1983–84 revealed that mass releases of these covered 12 million ha in the USSR, 1 million in China, 0.35 million in the

*Respectively: International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India, and Indian Agricultural Research Institute, New Delhi, India.

USA, 0.13 million in Peru, and smaller areas in at least nine other countries (Anon. 1984). In India, however, augmentation of natural enemies for pest control has received attention only in the last five decades, and the only major commercial augmentation program currently practiced is with *Trichogramma* spp. for the control of sugarcane borers (Sithanantham et al. 1982).

Heliothis species are recognized as pests of many crops of the tropics and subtropics (Reed and Pawar 1982). There are at least three species of *Heliothis* in India, but *Heliothis armigera* (Hübner) is by far the most important, for it is a widespread and damaging pest of many crops, particularly of cotton (*Gossypium* spp.), pulses, and several vegetables. This pest is known to cause enormous losses and there is some awareness of the dangers of relying solely on insecticides for its control. Nagarkatti (1982) reviewed the scope for utilization of biocontrol against *Heliothis* spp. in India. Although field releases to augment native parasites and predators of this pest have been carried out on an experimental scale on several crops, there are no reports of large-scale augmentation of natural enemies, nor has any commercial exploitation of biocontrol agents yet been undertaken for the management of this pest in India. This paper will review some of these release experiments in an effort to identify the problems and prospects for augmentation of natural enemies of *Heliothis* spp. in India.

EXPERIMENTS TO AUGMENT THE NATURAL ENEMIES OF *HELIOTHIS* SPP. IN INDIA

Experiments to augment the natural control of *Heliothis* spp. in India were done by inundative releases of parasites and inoculative releases of exotic parasites. There are no published reports evaluating the augmentation of predators, except in the provision of perches in chickpea (*Cicer arietinum* L.) fields, which were found to increase the predatory effects of birds on *H. armigera* larvae in that crop (AICPIP 1980). There have been efforts to mass rear *Chrysopa scelestes* Banks (Krishnamoorthy and Nagarkatti 1981) but there are as yet no attempts to assess the benefits of releasing these against *Heliothis* spp. in fields.

Inundative Release Experiments

Most inundative release experiments have utilized either the native egg parasite, *Trichogramma chilonis* Ishii (Patel 1975), or the exotic *Trichogramma brasiliensis* (Ashmead), which was introduced to India in 1968 (Sankaran 1974) and is now reared in several laboratories.

On cotton

Field tests using several natural enemies of bollworms have been reported from Ganpatpura in Gujarat state (Anon. 1985). In 1982 and 1983 fortnightly releases of the bioagents were made in a "biocontrol" field of 0.8 ha of cotton, in which two sprays of dimethoate has been made to control sucking pests. For comparison, another field was chosen as a control in which insecticides were regularly used against bollworms, which included *H. armigera, Earias vittella* (F.), and *Pectinophora gossypiella* (Saunders).

In 1982 the bioagents released against *H. armigera* were *Chelonus blackburni* Cameron (250,000), *T. chilonis* (20,000), and *Menochilus sexmaculatus* (F.) (1200), in addition to five sprays of *Heliothis* nuclear polyhedrosis virus (NPV). Egg parasitism was 40% in the biocontrol field and 0% in the insecticide-treated field. Collections of larvae showed no establishment of the released larval parasites. However, the NPV spray caused 62% larval mortality.

In 1983 the bioagents released were *Bracon hebetor* Say (11,258), *C. blackburni* (54,285), *T. chilonis* (250,000), *M. sexmaculatus* (2120), and *Chrysopa* sp. (2050 larvae plus 2614 adults). In addition, eight sprays of the *Heliothis* NPV were also applied in this field. The level of egg parasitism averaged 64% and larval parasitism due to *C. blackburni* was 5%. In addition, 30% larval mortality occurred due to NPV. *B. hebetor* was not recovered. Parasitism of *H. armigera* eggs averaged 64%.

Unfortunately, the direct effects of the released parasites could not be determined in either of these years, in the absence of an untreated control plot. The insecticide-treated control field had less bollworm damage than the biocontrol field in both years. The net profit was greater from the insecticide-treated field in the first year, but in the second year the profit from the biocontrol field was about the same as that from the insecticide-treated field.

On tomato

During 1973-74, four fields of tomato (*Lycopersicon esculentum* Mill.), 0.2 ha each, were chosen for experimentation in Sadanapura village in Gujarat state (Patel 1975). In the first of these fields 25,000 *T. chilonis* were released every 10 days throughout the season. In the second field 50,000 *T. chilonis* were released each week. The other two fields were untreated controls. The mean egg parasitism rates recorded were 36% in the first field and 60% in the second, compared with 6% and 26% in the two control fields. Fruit damage was recorded only in the second field, where it averaged 12%, and in the corresponding control field the average was 34%.

During 1974–75, a similar trial was conducted, with releases of 50,000 *T. chilonis* per 0.2 ha/week (Patel 1975). The mean egg parasitism in the release field was as high as 76% versus 2% in the control field. A distinct

reduction was also seen in the larval population and the fruit damage was only 8% in the release field, compared with 26% in the control field.

Inundative releases of *T. brasiliensis* have been tested against *H. armigera* on tomatoes at Bangalore in Karnataka state (Anon. 1985). In 1984, five weekly releases of about 10,000 to 12,000 *T. brasiliensis*/ha per week were made in a farmer's field of about 1 ha that was heavily infested by *H. armigera*. The parasitism of *H. armigera* eggs averaged 36%, with a peak of 63%. In another field of 0.4 ha, where *H. armigera* populations were much lower, the release of a total of 30,000 *T. brasiliensis* resulted in 9% parasitism in the eggs. There were no control plots in these experiments, so the effects of parasitism on larval populations, damage, and yield could not be determined.

On potato

Patel (1975) reported a trial in Gujarat state in 1975, in which 50,000 *T. chilonis* were released per week on 0.2 ha of potato (*Solanum tuberosum* L.) infested with *H. armigera*. The mean egg parasitism was 81% in the treated plots of 57% in the control. The mean number of *H. armigera* larvae per 100 shoots was 20 in the control plot but only 6 in the treated plot. These data were based on five weekly samples.

It is probable that populations of *Heliothis* spp. larvae on tomatoes and potatoes include both *H. armigera* and *H. assulta* Guenée, for the latter insect is known to feed on solanaceous crops and is not easily distinguished from the more common *H. armigera*.

On lucerne

Near Anand in Gujarat, releases of *T. chilonis* were made at the rate of 250,000/ha per week in a 0.2 ha plot of lucerne (*Medicago sativa* [L.]) for 7 weeks in March–April (Patel 1975). The mean parasitism of *H. armigera* eggs in March was 44% in the treated and 31% in the control plots, but in April it declined to 5 and 1%, respectively, probably due to the high temperatures, which often exceeded 38°C.

On chickpea

Inundative releases of *T. chilonis* were tested on chickpea in Gujarat state (Patel 1975). However, no *H. armigera* eggs were parasitized. The acidic exudates of the plants were suspected to be a factor resulting in the failure of the parasites. The deterrent role of exudates on the activity of *Trichogramma* spp. was later confirmed in studies at ICRISAT (Bhatnagar 1981).

Inoculative Release Experiments

In India, inoculative releases have been made of some exotic egg and larval parasites of *Heliothis* spp., mostly during the last decade.

Trichogramma brasiliensis was reported to have established after inoculative releases on cotton in Maharashtra state (Raodeo et al. 1978). Promising results of *T. brasiliensis* establishment are also reported following releases on tomato near Bangalore, Karnataka state (Mani and Krishnamoorthy 1983).

Inoculative releases of the egg-larval parasite, *C. blackburni* (2637) on cotton (July to September 1977) in Maharashtra, resulted in recoveries 8–10 days after release on *H. armigera* as well as on the other two bollworms, *E. vittella* and *P. gossypiella* (Sarkate et al. 1978). Prasad et al. (1982) attempted inoculative release of *C. blackburni* on chickpea in Haryana state during 1979–80 and obtained evidence of the parasite being active in the field after a week.

There are several reports of laboratory multiplication and field release of the tachinid larval parasite, *Eucelatoria bryani* Sabrosky, which was imported to India from the USA in 1978. Releases into field cages over infested pigeonpea (*Cajanus cajan* [L.] Millsp.) and chickpea at ICRISAT Center, near Hyderabad, during 1979–80, resulted in parasitism of *H. armigera* larvae (12% on pigeonpea, 3% on chickpea). In subsequent years (1980–83), several hundred mated females were released on unsprayed crops of pigeonpea and chickpea at ICRISAT Center. While parasitism was observed in *H. armigera* larvae within a week after release, subsequent recovery later in the season was very rare. In an unpublished study comparing the generation time of *E. bryani* with that of *H. armigera*, it was found that if there are nonoverlapping generations of the host, the parasite will be asynchronous with the susceptible stage of the host in the generations following release. Further, the very high temperature in summer (often exceeding 40°C) was detrimental to the parasite.

However, releases of *E. bryani* on tomato around Bangalore were more promising. Pawar et al. (1981) released this parasite in four fields in the district from January 1979 to April 1980 and subsequently recovered parasitized larvae in all these fields. Mani and Krishnamoorthy (1983) released *E. bryani* in tomato fields near Bangalore during 1980 and 1981 and recorded parasitism of up to 8%. The availability of irrigated crop hosts such as tomato during most of the year in the surrounding areas probably ensures adequate availability of *H. armigera* larvae for the parasite to survive. Also the cooler climate in this location during most of the year is relatively more favorable for the survival of *E. bryani*.

Recent Large-scale Releases

Efforts to release large numbers of parasites and predators of *H. armigera* on crops in different parts of the country are being made by the Central Biological Control Stations of the Government of India. During 1984–85, six of these stations—Bangalore, Burdwan, Faridabad, Solan, Sriganga-

Table 1. Parasites and predators of H. armigera *released in various crops at six biological control stations in India, 1984–85.*

Parasite	
Egg parasite	*T. brasiliensis* Ashmead
	T. chilonis Ishii
	T. pretiosum Riley
Egg-larval parasite	*Chelonus blackburni* Cameron
Larval parasite	*Bracon brevicornis* Wesmael
	B. hebetor Say
	Eucelatoria bryani Sabrosky
Predator	
	Chrysopa sp.

nagar, and Surat—have together treated a total area of about 230 ha of maize (*Zea mays* L.), pigeonpea, chickpea, tomato, some other vegetables, and marigold (*Tagetes* sp.), by releasing several parasites and predators against *H. armigera* (Table 1) (India: DPPQS 1985).

These releases, however, do not appear to have been backed up by economic evaluation of the impact on the crops.

POTENTIAL FOR AUGMENTATION AND SUGGESTED FUTURE RESEARCH STRATEGIES

To evaluate the potential for economic use of inundative releases of natural enemies, it is necessary to test the inputs in large-scale replicated tests in farmer's fields. Such experimentation will be costly. However, without such trials, there is no hope of advancing this element in *Heliothis* spp. management in India. Past research has been diluted over many pests, crops, and geographical areas. To make real progress we must identify a few pest/crop situations that appear to have the greatest potential for biocontrol use.

Cotton would appear to be a priority crop on which to work, given its high value, the progressive outlook of cotton farmers in general, and the availability of a cooperative infrastructure to support such efforts. However, the low economic threshold on cotton will necessitate the use of insecticide. Therefore, an integrated approach to combine the two elements has to be worked out.

Alternatively, the large losses caused by *H. armigera* on pigeonpea and chickpea may suggest that these crops are suitable for biocontrol evaluation. Here, only a few farmers use insecticide, so it may not be necessary to integrate biocontrol and insecticide use. But the low level of egg parasitism on these two crops needs to be counteracted.

The thrust of future augmentation research should be on aspects of

immediate and practical use in the field situation. Some of these aspects are discussed below.

Evaluating the Potential of Native Natural Enemies

The common parasites of *H. armigera* in India are: *Trichogramma chilonis, Campoletis chlorideae* Uchida, *Bracon brevicornis, Eriborus* sp., *Carcelia illota* Curran, and *Goniopthalmus halli* Mesnil. Common predators include wasps, chrysopids, bugs, spiders, and birds. While the levels of parasitism by the common parasites have been estimated in several regions, predation effects have not received attention, probably because their influence is difficult to estimate in the field. Empirical estimates have been made of the predation potential of *Chrysopa scelestes* (Krishnamoorthy and Mani 1982), wasps (Pawar and Jadhav 1983), spiders and birds (ICRISAT 1984; ICRISAT unpublished); such efforts should be extended to the other common predators in different regions.

Scattered results are available on the contribution of native parasites and predators to the mortality of *H. armigera* in different crops (Bilapate 1981), the optimal ratios of parasite (*C. chlorideae*) to *Heliothis* spp. numbers for ensuring effective parasitism (Nikam and Basarkar 1982) and of the timing of field releases of a parasite (*T. chilonis*) against *H. armigera* (Somchoudhury and Dutt 1980). Similar data must be assembled in different crops and regions, so that the rationale for augmentative releases of natural enemies and evaluation of their impact can be more dependably developed. The search for races/biotypes of native parasites better adapted to the field conditions should also be taken up, as exemplified by the work done by Abraham and Pradhan (1976) on *T. chilonis* for adaptation to high temperature and low humidity.

Host-Plant Influence

The direct influence of host plants on the activity of natural enemies of *Heliothis* spp. needs some consideration. For instance, field parasitism of eggs by *T. chilonis* was substantial on sorghum (*Sorghum bicolor* [L.] Moench) (about 25%) but very insignificant (0.1%) on pigeonpea (Bhatnagar et al. 1982). Manjunath et al. (1970) reported that egg parasitism of *H. armigera* on marigold intercropped with tomato was much greater than on tomato and on other crops in the vicinity. Naganna Goud (1979) found natural parasitism of *H. armigera* eggs by *Trichogramma* spp. (*T. chilonis* and *T. acheae*) was high (51%) on cotton but very low (5%) on okra (*Abelmoschus esculentus* L.). Yadav and Patel (1981) found *T. chilonis* parasitism of *Heliothis* spp. eggs to be greater (71–98%) on potato than on lucerne (30–48%) and tomato (10–52%). At ICRISAT, the range of native larval parasites of *Heliothis* spp. and their relative dominance have been found to differ between crops (Bhatnagar et al. 1982).

Some preliminary results are also available on genotype differences in pigeonpea influencing the egg and larval parasitism of *H. armigera* at ICRISAT. If agronomically acceptable cultivars which also favor the activity of natural enemies can be identified, we may be able to derive greater benefit from augmentation strategies.

Integration with Insecticide Use

In crops where insecticides are necessarily used, it will be useful to choose the chemicals that are less detrimental to important natural enemies. Several recent laboratory studies on the relative toxicity to *Trichogramma* spp. of commonly used insecticides have been carried out in India (Navarajan Paul et al. 1976, 1979; Sithanantham et al. 1978; Dutt and Somchoudhury 1980; Sithanantham and Navarajan Paul 1980). Concurrent field evaluations of the toxicity of insecticides against bollworms (including *H. armigera*) and on the important natural enemies on cotton have helped to identify relatively safer insecticides like endosulfan and phosalone (Jawale 1978; Dhurve et al. 1980). Patel (1983) found that the judicious use of carbaryl, methyl parathion, or endosulfan at low doses during October–November on cotton not only controlled the pests satisfactorily but also minimized the adverse effects on *Trichogramma* spp. parasitism of *H. armigera* on cotton. More research on need-based application of insecticides, with action thresholds developed for *Heliothis* spp., would indirectly benefit any augmentation efforts as well as IPM in the many target crops where insecticide use is now common.

Mass Production and Economics

Mass production of natural enemies for managing *Heliothis* spp. populations presents particular problems relating to timely supplies. Being polyphagous and mobile, *Heliothis* spp. can build up their populations rapidly on individual crops and even the first generation may cause substantial damage. Supplies of the natural enemies for field release have to be available soon after the eggs or early larval stages of *Heliothis* are noticed on the crop. This creates problems in mass production and supply.

Mass production of *Trichogramma* spp. is relatively cheap and easy. Some of the braconid larval parasites can be mass reared on more easily reared substitute hosts such as *Corcyra cephalonica* Stainton, and so can be readily mass produced. The mass rearing of other larval parasites, especially the solitary ones, is considered laborious and uneconomical (Nagarkatti 1982), as it involves mass rearing of *Heliothis* spp., which is both difficult and expensive. An attempt to rear *Campoletis chlorideae* on larvae of *Spodoptera litura* (F.) has recently been reported as successful (Anon. 1985), and we should evaluate whether this might help in economi-

cal mass production. Krishnamoorthy and Nagarkatti (1981) have developed a modified mass-rearing technique for the predator *Chrysopa scelestes*, and the economics of mass production of this predator has been recently assessed (Anon. 1985).

Successful augmentation of the natural enemies, particularly by inundation, depends largely on cheaply and readily available mass-reared bioagents. A commercial mass-production center commissioned recently at Bangalore has encouraged optimism about the availability of some bioagents. *T. chilonis* is one of the several natural enemies being mass produced at this center. Besides *H. armigera*, this insect parasitzes seven other lepidopteran pests of cotton and sugarcane. The present price of *T. chilonis* at this center is about U.S. $75 per million. Probably, the actual price on a no-profit basis would be much lower. At some stage, a decision will have to be made whether the mass production and supply of these bioagents should be a commercial practice or if it should be supported by the government as a social service. Fortunately, in India, human labor is abundant enough to support small production centers that are less sophisticated but are labor intensive. These may be established as a network in rural areas to cater to clusters of villages.

CONCLUSIONS

Field trials to evaluate the benefits of augmentation of parasites and predators of *Heliothis* spp. in India have been very limited in number. Further, these efforts have been largely *ad hoc* and lack comprehensive data on efficacy or economic benefits. It is important that mass-reared natural enemies of consistently high quality are released in sufficient quantity in inundative experiments and their impact assessed in large-sized "release" and "no-release" blocks, with adequate replication. The economic benefit of the releases must be assessed by quantifying the extent of pest suppression, damage reduction, and effects on yield. Inoculative releases should be tested across differing crop and climatic situations to determine favorable situations. We should stagger these attempts over years and at each time concentrate our resources in a well-defined target area on chosen crop(s) where the maximum chance of success is expected. Augmentation will be easier to practice on crops where insecticides are not used. On high-value crops, where insecticide use is unavoidable, we should identify ways and means of minimizing the adverse effects of insecticides on the natural enemies that are released for augmentation. Efforts should also be made to enhance the efficiency of mass production and so make it cheaper, besides developing the infrastructure that can ensure timely and adequate supplies of the natural enemies.

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Protection and Utilization of the Principal Natural Enemies to Control *Heliothis armigera* in China

C.Y. Fang, S.G. Wen, and F.Q. Hu*

ABSTRACT

The bollworm, *Heliothis armigera* Hübner, and the cotton aphid, *Aphis gossypii* Glover, are the most important insect pests in the Yellow River Valley of China. According to preliminary results, there are more than 50 species of parasites and predators of the bollworm. Many of these predators attack the cotton aphid, too.

The second generation of the bollworm is often maintained at sub-economic population levels by the natural enemies. The cotton aphid is controlled by seed treatment with a systemic insecticide and by the use of coccinellids.

The bollworm, *Heliothis armigera* Hübner, is distributed throughout the cotton-growing areas of China. There are three to eight generations annually, with the number increasing from north to south. Four generations occur annually in the Yellow River Valley.

The first egg-larval generation occurs on wheat, legume crops used as green manure, and on the plant *Abutilon theophrasti.* The second generation of larvae occurs on cotton and to a lesser extent on tomato. The third larval generation occurs on cotton, maize, and legumes; the fourth larval generation is found on cotton, maize, legumes, and sunflower. The second and the third larval generation have most often in the past required insecticidal application for their control (Cotton Research Institute, Chinese Academy of Agricultural Sciences 1983).

The cropping system is similar throughout the cotton-growing area of the Yellow River Valley. In the spring, the area planted to wheat predominates, comprising over 50% of the total cropping area. Cotton is planted on 10 to 30% (approximately 20%) of the crop area. The spring food crops,

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maize and sweet potato, occupy about 4% of the crop area and the remaining 20% of the area consists of vegetables and other crops.

The bollworm has a broad host range and is often found feeding on most of the crops in the area. Thus its natural enemies may also be found throughout the area. Occurrence of these natural enemies in the annually planted cotton depends on the maintenance of favorable conditions. Recent research at the Cotton Research Institute has concentrated on defining these conditions.

INTEGRATED PEST MANAGEMENT

Normally, cotton seedlings are damaged by aphids immediately after emergence from the ground. Four to five applications of insecticides may be required to control the aphids. These chemicals kill the natural enemies of *Heliothis* migrating into the cotton fields from adjacent wheat fields. Consequently, the second generation of egg-larval bollworm populations are not suppressed.

Winter wheat fields are important sites for predators to overwinter and reproduce. Their numbers may exceed 15,000/ha by 30 April (Table 1). Mid-May to late May are periods when predator populations peak in wheat fields. For example, 1,000 sweeps with a net (diameter = 33.33 cm) has resulted in 3,144 coccinellids, 49 phytoseeids, 30 nabids, 10 chrysopids, and 882 syrphids. These predators feed on pests, including the bollworm, that attack the wheat.

Bollworm larvae collected from the wheat fields and held in the laboratory have been found to be parasitized at rates of 16 to 47%. Predominant parasite species were *Campoletis chlorideae* Uchida and *Microplitis* sp.

Table 1. Number of natural enemies of Heliothis armigera *found in the cotton-growing region, Yellow River basin, China*

Date of Survey	Number/ha		
	1982	1983	1984
April 10	1,720.5	9,810	0
15	8,595	18,405	0
20	8,805	13,005	6,000
25	4,005	—	—
30	22,005	38,010	22,005
May 5	42,615	—	—
10	86,445	68,025	53,025
15	31,665	19,365	3,690
20	49,335	23,235	8,550
25	47,580	11,820	15,060
30	10,440	8,760	13,035

Other natural enemies found include *Netelia ocellaris* and several species of syrphids: *Exorista japonica, E. civilis,* and *Gnidia bimaculata.*

When the wheat senesces and is harvested during mid-May to late May, the predators and parasites are forced into the adjacent cotton fields. Therefore it is important to avoid foliar application of insecticides to seedling cotton. Instead, aphids may be controlled with systemic insecticides, particularly carbofuran 3% granules, applied in the furrow with the cotton seed, at planting time.

During 1978 to 1980, application of the systemic insecticides carbofuran and phorate were compared for aphid control in seedling cotton. Carbofuran, 3% granules applied in-furrow at planting, 22.5 to 30 kg/ha, gave the best aphid control; seedlings thus protected showed no leaf curl from aphid feeding even 45 to 50 days after planting; i.e., until late May. Although aphid numbers begin to increase at this time, coccinellids such as *Coccinella septempunctata* and other natural enemies move into the cotton to suppress the aphid populations (Fang Changyuan et al. 1981).

SAMPLING FOR PESTS AND NATURAL ENEMIES

Surveys on insect pests and their natural enemies in wheat fields are conducted from 10 April to 10 May. Thirty random samples are taken at five points over a 1 to 2 m² area. From 15 May to 5 June, scrutiny is done by sweepnet (diameter = 33.33 cm), with 1000 sweeps per field. Sampling is done at 5-day intervals. Bollworm larvae collected are classified by instar, and the species and number of natural enemies collected are also recorded. The bollworm larvae are held in the laboratory to assess the level of parasitism.

Surveys in cotton fields begin at the seedling stage. Samples are taken at five points in each of four to six carbofuran-treated fields, at 5-day intervals up to 10 June and at 3-day intervals thereafter because of the occurrence of second-generation bollworms. One hundred plants in each cotton field are observed. The number of cotton aphids, number of bollworm eggs and larvae, and species and number of natural enemies are recorded.
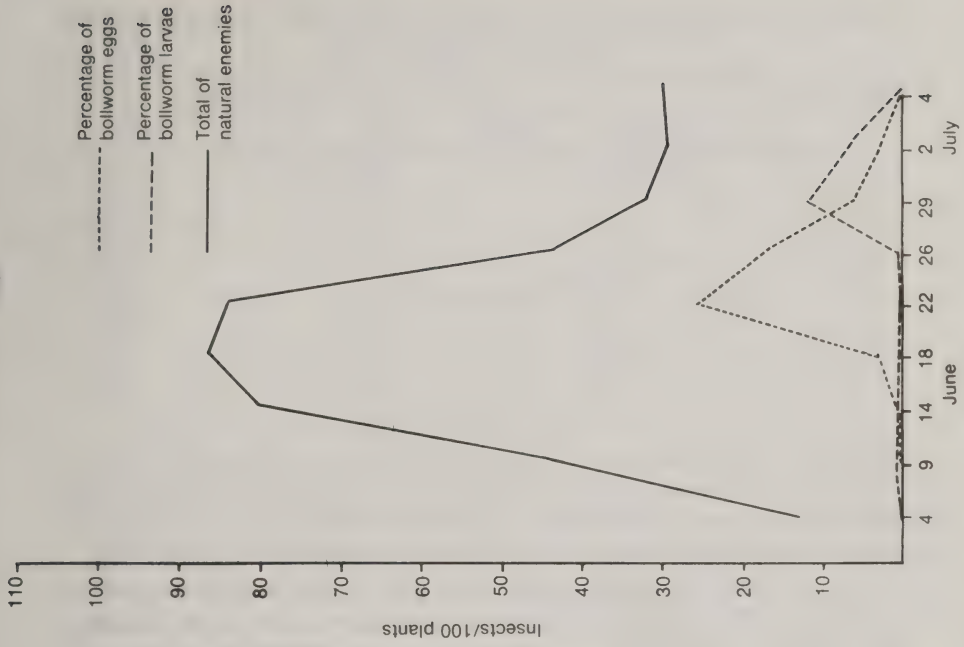
DECISION-MAKING

In early June, the number of natural enemies ranges from 20 to 286/100 cotton plants. Once the second generation of bollworm occurs, the complex of natural enemies changes.

Survey in the Anyang District of Henan Province revealed that the total natural enemy population was composed of coccinellids (36.8%),

1981

Percentage of
bollworm eggs

Percentage of
bollworm larvae

Total of
natural enemies

Insects/100 plants

1982

Percentage of
bollworm eggs

Percentage of
bollworm larvae
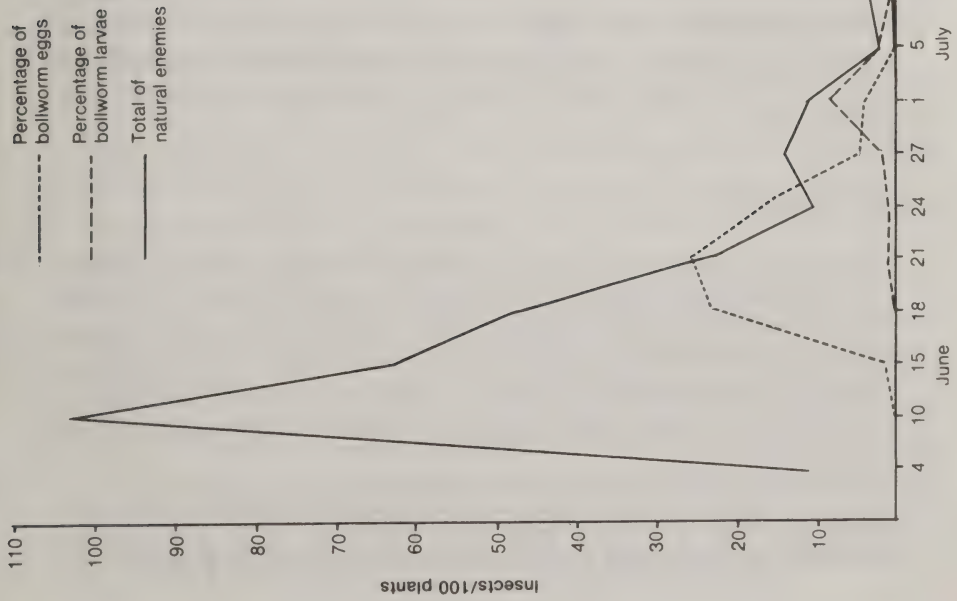
Total of
natural enemies

Insects/100 plants
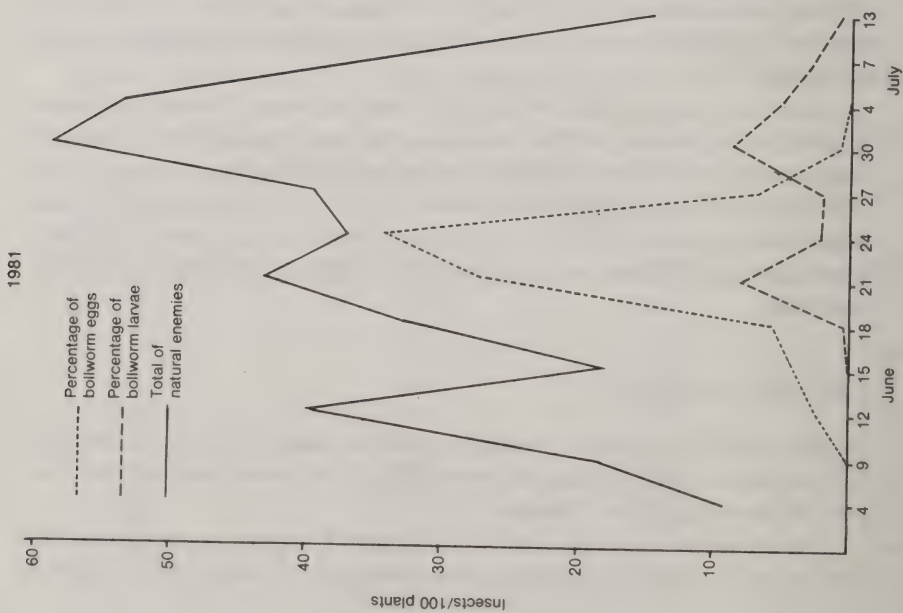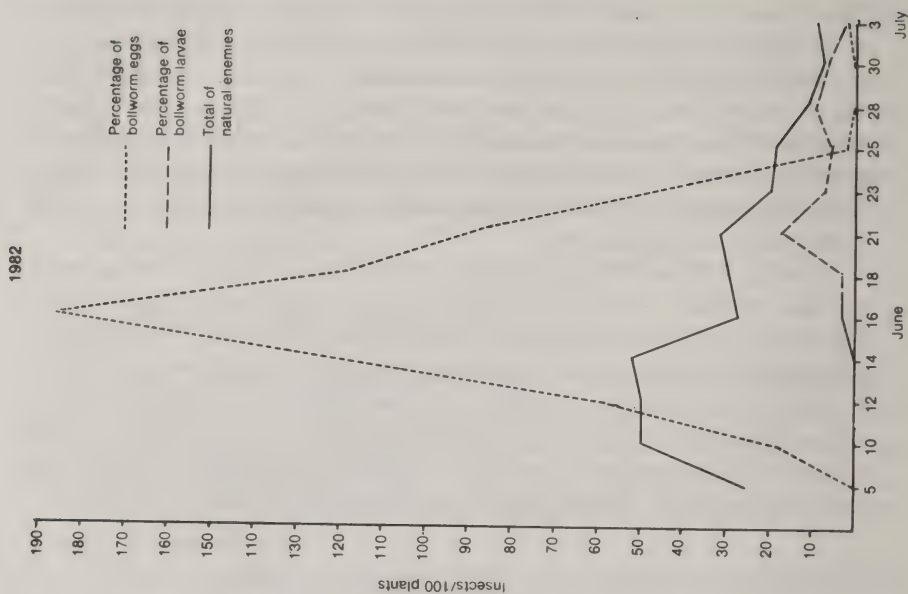
Figure 1. Fluctuation of bollworm and principal natural enemy populations in cotton fields not treated with pesticides in China, 1981–1984.

Table 2. Ratio of principal natural enemies to bollworm in cotton fields,
Yellow River basin, China

Date of survey	Ratio of natural enemy to bollworm		
	1982	1983	1984
June 10	1 : 0.4	1 : 0	1 : 0.01
15	1 : 2.4	1 : 0.02	1 : 0.01
18	1 : 4.1	1 : 0.5	1 : 0.03
21	1 : 3.4	1 : 1.1	1 : 0.3
24	1 : 2.6	1 : 1.7	1 : 0.4
27	1 : 0.8	1 : 0.4	1 : 0.2
30	1 : 0.8	1 : 1.08	1 : 0.5
July 2	1 : 0.4	1 : 1	1 : 0.25
5	1 : 0.2	1 : 0.3	1 : 0.05

spiders (34.1%), *Orius* spp. (15%), nabids (12%), and chrysopids (1%). At
Zhucheng in Shandung Province, survey showed that natural enemy
populations were composed of coccinellids (53.6%), chrysopids (26.3%),
spiders (10.4%), and braconids (9.7%) (Wu Qinlei and Teng Jun 1981).

The ratio of natural enemy to bollworm in samples taken from 1982 to
1984 was 1 : 4 to 1 : 0.01 (Table 2). Natural enemy numbers were as high as
300/100 plants. Principal natural enemies in cotton fields were *Propylaea
japonica* (Thunberg), *Hippodamia variegata* Goeze, *Nabis sinoferus*
Hsiao, *Orius minutus* L., *Chrysopa sinica* Tgeder, *Coccinella septempunc-
tata* Wesmael, *Erigonidium graminicolum* Sund., *Misumenops tricuspi-
dotus* (F.), and *Neoscoma donenitzi* (Bois et Str.).

These natural enemies often maintain the number of bollworm larvae
exceeding the third instar at less than 5/100 plants (Figure 1). Conse-
quently, the economic threshold for initiating insecticide treatments has
been set at 20 young larvae/100 plants (Wen Shaogui and Fang Chan-
gyuan 1985).

DISCUSSION

The cotton-growing area of the Yellow River Valley in China is a major
wheat-producing area as well. The cotton is interplanted with the wheat.
Where cotton is planted as a monoculture, low numbers of natural enemies
are present, and the bollworm is not suppressed below economic levels.
Therefore, maximum effort is made to strip-crop the cotton and grain, in
10-ha fields, so that the natural enemies can readily move from grain fields
to cotton fields.

The natural enemies are spared in early-season cotton fields by avoid-
ing foliar application of insecticides for aphid control. The cotton aphid is
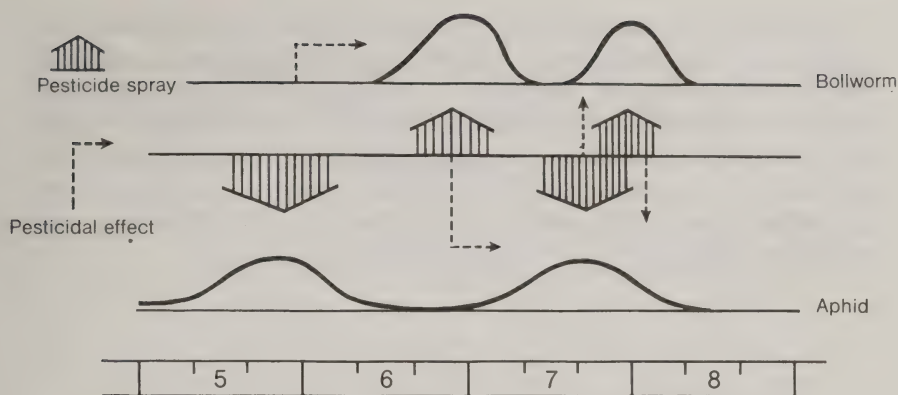controlled until late May by carbofuran applied in-furrow at planting.

Figure 2. Interaction of cotton aphid and bollworm in pest insect control in China.

Natural enemies, particularly coccinellid *C. septempunctata*, often maintain the aphid at subeconomic levels until the occurrence of the second generation of the bollworm. Rapeseed and maize are interplanted in the cotton fields to provide food and shelter for the natural enemies. These plants also serve as trap crops for pests such as the black cutworm, corn borers, and the bollworm.

Successful biological control of the bollworm depends on management of other pests, particularly cotton aphids. The two peak infestations of the cotton aphid alternate with the second and third egg-larval bollworm generations in cotton (Figure 2). Foliar applications of insecticides for control of aphids eliminates natural enemies normally attacking the bollworm. Consequently, more insecticide applications are necessary for control of the bollworm, and this cycle continues through the season.

Sparing natural enemies in wheat fields and cotton fields through the use of selective insecticides, selective application methodology, and reduction of insecticide application are important aspects of the Chinese integrated control system for the bollworm in cotton. The aphid and bollworm are viewed as the most important pests, and secondary pests are considered subordinate to the requirements of the system.

Protection of natural enemies in the wheat fields is of paramount importance. For example, diflubenzuron is used instead of organophosphorus compounds to control the armyworm *Leucania separata* Walker (Ni Hanxiang and Jin Dasheng 1983). And other insecticides are suggested for wheat aphid control. Use of soil-applied systemic insecticides for control of aphids in cotton eliminates the need to use foliar applications that would destroy predator populations. These predators suppress the aphid and bollworm populations in cotton. Finally, under high humidity conditions caused by early onset of the rainy season, aphids may be suppressed by the fungus *Entomophthora aphidis* Hoffman.

Decision-making technology is being developed that simultaneously considers the status of the pest and natural enemy populations. Survey and prediction technology are being joined. These integrated control measures have been extended over about 150,000 ha so far. Considering control of the bollworm second generation alone, the area requiring insecticide applications has been reduced by one-third to one-half, and one to two applications have been eliminated, to the advantage of both the farmer and the environment.

Behavior-modifying Chemicals to Increase the Efficacy of Predators and Parasitoids of *Heliothis* spp.

Michael A. Keller and *W. Joe Lewis**

ABSTRACT

Semiochemicals are important cues influencing host selection by insect natural enemies of *Heliothis* spp. Chemicals produced by plants guide foraging entomophagous insects to suitable habitats where volatile and contact chemicals from host insects provide cues for the location of hosts. These behavior-modifying chemicals potentially can be utilized to screen exotic species prior to colonization and to improve rearing techniques. In addition, semiochemicals could be used as stimulants prior to release or be applied directly in the field to promote greater natural-enemy-induced mortality. Current and future studies on the behavioral responses of entomophagous insects to kairomones and synomones should improve prospects for the development of practical techniques for managing their behavior in the field.

INTRODUCTION

Classical biological control is a preferred method of pest suppression because it is economical, long-lasting, self-renewing, and environmentally innocuous (Rabb et al. 1984). However, implementation has been successful only in approximately one-third of all attempts (Hall and Ehler 1979; Beirne 1985). This is especially true for pests of annual row crops, such as *Heliothis* spp. For example, in spite of being attacked by a large number of natural enemies (Whitcomb and Bell 1964, Lewis and Brazzel 1968, Shepard and Sterling 1972, Burleigh and Farmer 1978), both *Heliothis zea* (Boddie) and *Heliothis virescens* (F.) continue to be major pests in the southern USA (Warren 1979). Techniques for improving the level of biological control by increasing entomophage densities also have had only limited success. For example, inundative releases of egg parasitoids in the

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genus *Trichogramma* have been successful in some cropping systems (e.g., tomato: Oatman et al. 1978) but not in others (e.g., cotton: Ridgway and Morrison 1985). The future success of biological control of *Heliothis* spp. may depend, in part, on the development of new techniques and strategies for the employment of entomophagous insects.

In this paper, we examine possibilities for the utilization of behavior-modifying chemicals (Nordlund 1981) to improve the efficacy of natural enemies in biological control. First, we describe the roles that semiochemicals play in the foraging behavior of natural enemies and review several examples of the types of chemical cues that influence host selection by natural enemies of *Heliothis* spp. Second, techniques for studying the influence of contact and volatile chemicals on behavior are described. Third, the utilization of behavior-modifying chemicals in screening exotic species for potential colonization in new localities, in rearing, and in the pre-release handling of beneficial insects is discussed. Fourth, we examine the potential for manipulating natural-enemy behavior in the field. In addition, semiochemicals could be utilized to monitor population levels of natural enemies.

ROLES OF SEMIOCHEMICALS IN HOST AND PREY SELECTION

The host selection behavior of insect parasitoids can be divided into four sequential steps: host-habitat location, host location, host acceptance, and host regulation (Vinson 1976). Prey selection by predators can be viewed as a similar process (Greany and Hagen 1981). The mobility and habitat preferences of natural enemies, as well as habitat availability, determine which habitat types will be searched by entomophagous insects (Vinson 1981, 1984). Volatile synomones (Nordlund 1981) released by plants appear to be important cues for locating suitable habitats (Read et al. 1970, Altieri et al. 1981. Elzen et al. 1983b). Once inside a suitable habitat, cues from the host, including feeding damage, host products (e.g., salivary secretions and frass: Lewis and Jones 1971; silk: Dmoch et al. 1985), and associated organisms (Greany et al. 1977) may direct natural enemies to their hosts or prey. Host acceptance is influenced, in part, by contact kairomones (Arthur 1981).

Numerous studies have examined the roles that semiochemicals play in host and prey selection by entomophagous insects that attack *Heliothis* spp. We cite here a few examples of different types of natural enemies and the chemicals that influence their behavior. Our goal is to illustrate the principles of host and prey selection rather than to review extensively the literature on natural enemies of *Heliothis* spp.

Several species of *Trichogramma* attack the eggs of *Heliothis* spp. (Hung et al. 1985). The widespread utilization of these insects in inundative

releases has led to numerous studies of the factors that influence rates of parasitization (Keller et al. 1985). Plant chemicals appear to be involved in habitat location since certain plant extracts can stimulate increased rates of parasitization (Altieri et al. 1981, Nordlund et al. 1984/85), but behavioral responses to these chemicals are not yet understood (Keller et al. 1985). The sex pheromones of some moths appear to have kairomonal activity for some species of *Trichogramma* (Lewis et al. 1982, Noldus and van Lenteren 1985b). Rather than directing foraging females to oviposition sites, these chemicals appear to indicate locations of moth activity, and hence areas where encounter with eggs is likely. Female *Trichogramma pretiosum* Riley respond in an undirected manner (flying individuals land and patterns of walking are modified) to the sex pheromone of *Heliothis zea* (L.P.J.J. Noldus, unpublished data). In close proximity to host eggs, moth scales trigger intensive searching behavior, which increases the probability of host encounter (Lewis et al. 1972, Noldus and van Lenteren 1985a). Host acceptance is influenced externally by accessory gland secretions (D.A. Nordlund, unpublished data) and internally by certain salts (Nettles et al. 1982).

Microplitis croceipes (Cresson) is a braconid that specifically attacks *Heliothis* spp. Females fly upwind to certain host plants of *Heliothis* spp. in a flight tunnel suggesting that plant chemicals play a role in habitat location (Y.C. Drost, unpublished data). Volatiles released at the site of larval feeding attract flying females (Drost et al., 1986). Sources of attractant odors appear to include plant damage and specific chemicals released by the feeding larva (P.O. Zanen, unpublished data). Walking individuals are influenced by contact kairomones present in frass, salivary secretions, (Lewis and Jones 1971), and silk (M.A. Keller, unpublished data).

Campoletis sonorensis (Cameron) is a larval parasitoid that attacks at least 27 species of Noctuidae (Lepidoptera), including *H. zea* and *H. virescens* (Lingren et al. 1970). Females are attracted to the flowers of some plants in an olfactometer, and will examine and probe plant parts, especially flowers, even in the absence of hosts (Elzen et al. 1983a). Flowers that elicit these responses release synomones that appear to be used in habitat location by this species (Elzen et al. 1983b). Odors from larval *H. virescens* on cotton leaves attract more female *C. sonorensis* than cotton leaves alone, suggesting that host volatiles serve as kairomones for host location (Elzen et al. 1984). Frass, silk, and cuticular chemicals influence host location and acceptance at close range (Schmidt 1974, Wilson et al. 1974).

Chrysoperla carnea (Stephens) is a generalist predator as a larva (New 1975), and will attack aphids, as well as eggs and young larvae of *H. zea*. While adults are not predaceous (Sheldon and MacLeod 1971), ovipositing females engage in habitat location behavior, which determines where larvae will search for prey. Adult *C. carnea* are attracted by caryophyllene,

Table 1. Sources of semiochemicals which can serve as host selection cues for natural enemies of Heliothis *spp.*

Plants:	Flowers (Elzen et al. 1983a, b)
	Leaves (Vinson 1975b, Elzen et al. 1983a)
	Actively growing structures (Flint et al. 1979)
	Damage (Dmoch et al. 1985, Loke et al. 1983, Elzen et al. 1983a)
Eggs:	Accessory gland secretions (Strand and Vinson 1982a)
	Ovariole secretion (Vinson 1975a)
Larvae:	Salivary/mandibular gland secretions (Vinson and Lewis 1965, Vinson 1968)
	Frass (Lewis et al. 1971, Wilson et al. 1974, Loke et al. 1983, Dmoch et al. 1985)
	Silk (Dmoch et al. 1985, Wilson et al. 1974)
Adults:	Sex pheromones (Lewis et al. 1982)
	Scales (Lewis et al. 1972)
	Excretion (Lewis et al. 1982)

a volatile released by actively growing plant tissues (Flint et al. 1979), and indole acetaldehyde (van Emden and Hagen 1976), an oxidation product of tryptophan that is present in aphid honeydew (Hagen et al. 1976). Close-range host location cues from *H. zea* appear to include moth scales (Nordlund et al. 1977).

The preceding examples illustrate the influence of semiochemicals on the foraging behavior of natural enemies of *Heliothis* spp. Sources of these semiochemicals are cataloged in Table 1 and include plants, eggs, larvae, and adults of *Heliothis* spp. Potentially, chemicals from each of these sources could be utilized to manipulate the behavior of natural enemies, although some may be less useful than others.

TECHNIQUES FOR STUDYING BEHAVIOR-MODIFYING CHEMICALS

The roles that chemical cues play in host and prey selection have been studied by means of a variety of techniques. Responses to nonvolatile chemicals have been studied by comparing rankings of behavioral responses (e.g., Lewis and Jones 1971, Wilson et al. 1974, Vinson 1975a), by examining effects on parasitization rates (e.g , Lewis et al. 1972), and through various quantitative measures of behavior (e.g., Beevers et al. 1981, Noldus and van Lenteren 1985a). Olfactometers and flight tunnels have been used to investigate behavioral responses to volatile cues. For example, diffusion olfactometers (e.g., Ferreira et al. 1979, Vet 1983a) measure the response of an insect to concentration gradients of test chemicals in still air. In contrast, Y-tube (e.g., Read et al. 1970) and four-field (Pettersson 1970, Vet et al. 1983b) olfactometers measure an insect's response to volatile chemicals in moving airstreams. The olfactometer described by Vet et al. (1983b) exposes the subject insect to four discrete

odor fields where it can move freely and sample different sources of volatiles before making a final choice for one chemical. Olfactometers can be used to screen a number of different sources without a detailed knowledge of the insect's behavior. However, insects confined in an olfactometer are not able to express certain behavioral responses in a normal way.

Flight tunnels permit insect subjects to maneuver as they would in the field to distant odor sources (Baker and Linn 1984). For example, van Emden and Hagen (1976) studied the response of *C. carnea* to breakdown products of tryptophan when the predators were tethered in a flight tunnel. Ethological studies of responses to host selection cues can be performed in flight tunnels when the natural enemy is not tethered. For example, the behavior of free-flying *Trichogramma exiguum* Pinto & Platner (Keller 1985) and of *M. croceipes* (Drost et al. 1986) has been studied in a flight tunnel.

The choice of a behavioral assay depends on the nature of the cues, the specific behavior being studied, and the goals of the experimenter. Where possible, assays that discriminate between different types of behavior should be utilized (Kennedy 1977). The use of such assays provides a better understanding of the nature of responses and should permit more rapid application of this information to the manipulation of natural-enemy behavior.

To date, research on parasitoid foraging has concentrated on host and parasitoid density, rates of parasitoid movement, and rates of host encounter (e.g., Morrison and Lewis 1981, Waage 1983), or solely on selected responses to the chemical cues (e.g., frass, larval silk) thought to direct beneficial insects in locating hosts (e.g., Dmoch et al. 1985, Wilson et al. 1974). These types of data need to be coupled with field studies that examine the normal sequence of encounters with host-selection stimuli, the responses of parasitoids to these stimuli, and a determination of how encounters with these cues increase the probability of locating hosts. Although laboratory experiments can provide important information regarding the behavioral responses of parasitoids to the semiochemicals involved in host selection, they cannot indicate how foraging time is allocated under field conditions. The influence on host mortality of each type of behavior-modifying chemical in the host selection sequence is unknown, since there are no published studies combining the behavioral responses of natural enemies to host selection cues with data on rates of parasitization or predation in the field.

Such research would permit an examination of how each act is integrated into the behavioral composite referred to as host selection. Data from these studies could then be utilized to improve models of crop/pest/natural-enemy systems (Stimac and O'Neil 1985). Research on the foraging behavior of natural enemies needs to be integrated by a strong

theoretical approach (Hassell 1978, Charnov and Skinner 1985) with other relevant data (e.g., host behavior and distribution, population structure, influence of competing species) to further develop an understanding of how searching efficiency influences the dynamics of populations of pests and their natural enemies.

We have initiated study of the behavior of *M. croceipes* in the field to elucidate how the behavior of individual parasitoids influences interactions (mortality rates and movement) between populations of parasitoid and host. In this work, data are collected on behavior of foraging wasps, their spatial location, plant substrates encountered, and time elapsed between behavioral events. In addition to examining sequential responses of the parasitoid to host-selection cues, we hope to address a number of questions regarding the foraging behavior of this species in the field. For example, how does oviposition influence subsequent behavior, how do parasitoids behave when no hosts are encountered, and, as a consequence of interactions between entomophage and pest behavior, which hosts are most susceptible to parasitization? With a better understanding of the mechanisms that govern foraging success, new techniques for improving biological control could be developed.

UTILIZATION OF SEMIOCHEMICALS IN BIOLOGICAL CONTROL

The utilization of semiochemicals potentially can improve every phase of a biological control program, from foreign exploration and insect rearing to field releases and post-release performance. After potentially useful entomophagous species have been identified by foreign exploration, semiochemicals can be employed to screen candidate species and strains before attempting colonization (Nordlund et al. 1981).

In general, conditions in a target crop-pest system differ from the region of origin of exotic natural enemies. When the target host species occurs on a different host plant, and/or the possibility of establishing new natural enemy-host relationships is being explored, the semiochemicals involved in host-habitat and host location are likely to differ. In some cases, these semiochemicals may not provide appropriate stimuli for foraging behavior in the selected natural enemy. For example, *M. croceipes* attacks *H. zea* larvae feeding on a variety of plants, including cotton and soybean, but not on maize. Recent laboratory studies suggest that maize volatiles interfere with host location cues (P.O. Zanen, unpublished data). Thus, the chemical environment provided by maize may not be suitable for host finding by *M. croceipes.*

Screening of natural enemies could involve relatively simple tests. Successful parasitism of a target host in a confined situation alone is

insufficient to indicate that a species will be suitable for release. The sequence of host selection behavior is circumvented when the two species are caged together. Testing should include any source of semiochemicals, either of plant or insect origin, that differ between the original and target ecosystems. Olfactometers (e.g., Vet et al. 1983a, b), flight tunnels (e.g., Drost et al., 1986), or ranked behavioral assays (e.g., Lewis and Jones 1971; Wilson et al. 1974) could be utilized in screening procedures. A comparative approach would appear most appropriate for such testing. Semiochemical sources from the ecosystem of origin could be used as a standard for comparison with new sources. To our knowledge, such screening for response of beneficial insects to semiochemicals has not been included in any biological control program. However, we believe that studies like this could indicate when introduction of a beneficial insect would not be appropriate for a target agricultural system, thereby saving further investment in a doomed effort.

Once natural enemy species have been selected for attempted colonization or periodic releases, semiochemicals could play a role in rearing. Insectary environments can be stressful to insects because they are unnatural in several ways. For example, insect movements are restricted, and the physical environment (e.g., lighting, humidity) may influence behavior and physiology adversely. By promoting foraging behavior, host-produced kairomones and plant-produced synomones could be used in rearing to reduce environmental stress, and thereby increase longevity and reproduction. For example, Nordlund et al. (1976) reared *T. pretiosum* on substrates either treated with an extract of scales from *H. zea* or left untreated. On treated surfaces, longevity increased from 11 to 12 days and realized fecundity increased from 81 to 111 progeny compared with untreated controls.

Often, host larvae are reared in the insectary on artificial diets. Frass from larvae reared on these diets has reduced kairomonal activity compared with that from larvae feeding on plant materials (Elzen et al. 1984). For example, *M. croceipes* showed reduced response to frass from *H. zea* reared on a pinto bean based diet compared with that from larvae reared on cowpea (Sauls et al. 1979). In other cases, factitious hosts are utilized to rear natural enemies because they are cheaper or easier to rear than natural hosts. In the future, hosts may in some cases be replaced by *in vitro* rearing techniques (Greany et al. 1984). Both factitious and artificial hosts will not contain many or all of the host selection cues that are associated with natural hosts. When cultural techniques include artificial diets, factitious or artificial hosts, the addition of semiochemicals could promote more intensive and frequent foraging activity than would occur in their absence, or stimulate acceptance of nonhosts.

For example, Strand and Vinson (1982b) used a host recognition

kairomone to induce *Telenomus heliothidis* Ashmead to oviposit into *Spodoptera frugiperda* (J.E. Smith) and *Phthorimaea operculella* (Zeller), two hosts that are suitable for parasitoid development but are usually rejected by foraging females. Thus, by incorporating certain semiochemicals into culturing techniques, the production of natural enemies could be increased. Behavior-modifying chemicals for use in rearing could be isolated from natural sources and held in frozen storage, or synthesized once the active components are identified.

Exposure of beneficial insects to host selection cues prior to release can influence subsequent behavior in the field in two ways. First, these stimuli typically promote intensified, localized search near the site of contact. Handling insects typically disturbs normal behavior and increases the tendency to disperse. Exposure to kairomones can reduce post-release dispersal by stimulating searching behavior. Both *M. croceipes* and *T. pretiosum* respond to such conditioning (Gross et al. 1975). An increase in the frequency of foraging among released entomophages should lead to increased rates of attack on hosts near the release site. The intensity of the searching response usually decays over time if no hosts are located. This response can be exploited at the time of release to promote searching behavior.

Secondly, some parasitoids learn to associate hosts with certain cues that are correlated with host encounters (Arthur 1966). When associative learning is involved in subsequent responses to host selection cues, exposure to these cues prior to release can influence entomophage behavior long after release into the field. Thus, exposing natural enemies to hosts in the presence of cues from the target agricultural system prior to release could improve prospects for colonization and biological control. In some species the timing of host encounters influences learning. For example, the polyphagous parasitoid *Exoristes roborator* (F.) exhibits a higher incidence, intensity, and duration of learned behavior when conditioned immediately after eclosion than when exposed to hosts 5 or 10 days after emergence (Wardle and Borden 1985).

IMPROVING THE PERFORMANCE OF NATURAL ENEMIES IN THE FIELD

Goals and Pest Research

Applications of semiochemicals to crop fields can be used to increase pest mortality by altering various aspects of natural-enemy behavior (Hagen et al. 1970, Lewis et al. 1972). These behavior-modifying chemicals could influence the behavior of beneficial insects in three ways: (1) individuals could be attracted into crop fields from surrounding vegetation, and (2)

dispersal away from the crop could be inhibited. These influences (1 and 2) should lead to an increase in natural enemy density in the target area, assuming other factors (e.g., rate of host location per female, parasitoid mortality) are equal. (3) Supplementing certain semiochemicals in target fields could promote more intensive, frequent, or prolonged search. This third influence under certain conditions may increase the rate of host attack per individual entomophage. Each of these possible effects could lead to an overall increase in host mortality inflicted by the manipulated natural enemy.

Hagen et al. (1970) first manipulated a bollworm natural enemy with a semiochemical by using an artificial honeydew to attract adult lacewings, *C. carnea*. These chemicals provided a kairomone and food supplement, both of which served to increase predator density. Indole-acetaldehyde, a breakdown product of tryptophan present in the yeast hydrolysate of the artificial honeydew, operated as a kairomone by attracting adult lacewings into target fields (van Emden and Hagen 1976). Other components of the artificial honeydew (sugar, water, whey-yeast hydrolysate) arrested movement of the lacewings and served as a nutritional supplement, thereby promoting oviposition. One week following an application of such a food spray to cotton, *Chrysoperla* egg density increased from 1 to 3 per plant and both the density of bollworm eggs and the numbers of damaged bolls declined (Hagen et al. 1970).

The use of semiochemicals from both plants and the host *H. zea* has been shown to increase rates of egg parasitization by *Trichogramma* in the field. For example, egg parasitization of eggs of *H. zea* by *Trichogramma* spp. increased from 13% in control plots to 22% in soybeans treated with an extract of scales collected from *H. zea* (Lewis et al. 1975). Similarly, the release of a synthetic blend of the sex pheromone of *H. zea* in cotton increased parasitization of eggs from 21% in control to 36% in treated plots (Lewis et al. 1982). Altieri et al. (1981) demonstrated that spraying various plant extracts onto crops can stimulate increased rates of parasitization. For example, parasitization of eggs of *H. zea* by *Trichogramma* spp. was 21% on soybean treated with an extract of *Amaranthus* compared with 13% on plants sprayed with water. The types of behavior that lead to increased rates of parasitization by *Trichogramma* in the presence of either plant extracts or sex pheromones are not yet understood.

Application of semiochemicals to crops has not been universally successful in stimulating increased rates of mortality. For example, the use of a uniform spray of moth scale extracts may reduce egg parasitization by *Trichogramma* spp. at low host densities, apparently by stimulating females to search too intensively where no hosts are present, thereby lowering their efficiency (Lewis et al. 1979). This problem can be overcome partly by impregnating particles of diatomaceous earth with the moth scale

extract to mimic natural scales (Lewis et al. 1979). When dispersed through a field, the treated particles intermittently stimulate searching by *Trichogramma*, rather than doing so continuously.

Since contact kairomones can reduce the searching efficiency of natural enemies in some circumstances, the use of volatile kairomones may be more useful in managing entomophage behavior without interfering with close-range host location behavior. Different volatile semiochemicals operate sequentially over long and short ranges in directing initially host habitat-location and subsequently host-location behavior of natural enemies. Plant chemicals, especially those released at sites of damage by larvae, may be the most promising choices of semiochemicals for manipulating searching behavior in the field if they can be used to stimulate persistent search without interfering with the location of hosts at close range. At present, little is known of the roles that volatile chemicals play in host/prey selection behavior, except that individuals are "attracted" (see Kennedy 1978) to certain odors (e.g., Hagen et al. 1970, Drost et al. 1986, Elzen et al. 1983a, b).

To date, the use of behavior-modifying chemicals to enhance the efficacy of natural enemies in the field has not been utilized in controlling target pests on a large scale. Techniques for dispensing these chemicals are not well developed, the understanding of their effects in agricultural systems is limited, and their influence on mortality rates is not always sufficient to control the target pest. For example, increases in rates of egg parasitization following applications of semiochemicals for *Trichogramma* spp. have been too small to control target populations of *Heliothis* spp. Following application of moth scale extracts, parasitization rates typically increase 10 to 20% (Lewis et al. 1975), while applications of plant homogenates or a synthetic sex pheromone blend have raised rates of parasitization by only 7 to 14% (Altieri et al. 1981) and 25% (Lewis et al. 1982), respectively.

Evaluation of the Efficacy of Behavior-modifying Chemicals

At least five criteria should be used when evaluating the potential for manipulating natural enemies with behavior-modifying chemicals. (1) Use of the chemicals should provide reliable pest control at high and low host density. (2) The techniques should be effective for both large and small fields. Previous tests have been conducted with relatively small fields or test plots. It is not clear if treatments will be equally effective in larger fields. For example, when a kairomone is utilized to attract natural enemies from areas surrounding the target field, the size of the natural enemy population will limit the size of field in which this technique will be effective. (3) Reliable sources of natural enemies must be available, since

natural populations often are not predictable. Habitat management may be necessary for some projects to ensure consistently high densities of natural enemies. Alternatively, techniques could be developed to permit mass culture and release of entomophages at optimal times as indicated by field scouting. The "quality" of these laboratory colonies (adaptation to physical environmental factors, behavioral responses to semiochemicals, mating behavior) must be monitored and maintained (Chambers 1977) to ensure that the entomophages will perform appropriately in the field. (4) When working with wild populations, there should be no decrease in the fitness of target natural enemies as a consequence of manipulating their behavior with semiochemicals (Price 1981). If so, genetic changes ("resistance") in populations of natural enemies could occur that would reduce their responsiveness to the semiochemicals employed. In practice, the influence of behavioral manipulation on the fitness of natural enemies cannot be determined with certainty until its practice is widespread in an agroecosystem. However, this possibility should be explored with the aid of simulation models as a part of developmental research when large-scale tests of new techniques are being considered. (5) Once developed, manipulation technologies must be economically competitive with other pest management techniques. Otherwise, there would be no incentive for adopting these practices.

Each type of behavior-modifying chemical typically can affect several organisms in the target agricultural system. In developing techniques for utilizing semiochemicals to improve the performance of natural enemies, the influence of these chemicals on nontarget organisms should be investigated. An initial consideration in testing field application should be to examine possible adverse effects on the target crop. For example, artificial honeydews are phytotoxic to cotton, and thus must be dispensed from feeding stations rather than applied directly to foliage (Hagen et al. 1970). Some chemicals serve to attract both the pest and its natural enemies. For example, sex pheromones of bark beetles attract their predators (Payne et al. 1984), and many natural enemies are presumably attracted to plants by the same chemicals that attract their hosts (Vinson 1976, Price et al. 1981). In some instance, the effects of a semiochemical on the density of a pest population could offset increases in the activities of natural enemies. Fortunately, some substances influence a number of entomophagous insects whose activities might be complementary in producing higher levels of pest mortality. For example, kairomones in artificial honeydews attract syrphids and lacewings (Hagen et al. 1970), and moth scales contain chemicals that promote intensified search in both *C. carnea* (Nordlund et al. 1977) and *Trichogramma* spp. (Lewis et al. 1972).

Integrated Approaches for Utilizing Semiochemicals

To achieve the desired level of pest suppression, some natural enemies will require manipulation with different types of cues ("multi-component approach"), while the use of substances that affect several groups of organisms in the target agricultural system will be necessary to control other pests ("multi-tactic approach"). The use of food sprays that have kairomonal activity (Hagen et al. 1970) is an example of the multi-component approach. Gross et al. (1981) developed techniques for applying eggs of *H. zea* killed with radiation to supplement naturally available hosts and other eggs parasitized by *T. pretiosum*, in combination with kairomones to manipulate rates of parasitization. Lewis et al. (1985) used these techniques and included extracts of *Amaranthus* foliage to manipulate populations of *T. pretiosum*, this increased rates of parasitization in cotton from 9% in control plots to 18% in areas treated with supplemental eggs, parasitized eggs, and behavior-modifying chemicals.

The existence of host pheromones that have kairomonal activity suggests that these chemicals might be utilized to impact pests negatively by disrupting their behavior and by promoting increased rates of attack by natural enemies in a multi-tactic approach (Greenblatt and Lewis 1983). For example, the sex pheromone of *H. zea* might be utilized to disrupt mating of the host, and to stimulate parasitization by *Trichogramma* spp. (Lewis et al. 1982). Also, the oviposition-deterring pheromone of *Pieris brassicae* L. might be utilized to reduce the density and survival of host eggs (Noldus and van Lenteren 1984a).

P.D. Greany et al. (unpublished data) increased the resistance of citrus fruit to attack by the Caribbean fruit fly, *Anastrepha suspensa* (Loew), by spraying the plant hormone gibberellic acid (GA) onto trees. The GA increased concentrations of certain essential oils in fruit peels resulting in lowered larval survival. Another type of multi-tactic approach to pest suppression would be to develop a spray that includes compounds that simultaneously increase crop defenses and provide habitat-selection cues for natural enemies. Perhaps crop plants could be stimulated to release new or greater quantities of volatile chemicals which attract natural enemies.

Another potential application for semiochemicals is in monitoring population levels of natural enemies. Caged virgin females or synthetic pheromones have been used to trap parasitoids (Lewis et al. 1971, Powell and King 1984) and predators (Aldrich et al. 1984) which attack *Heliothis* spp. In some cases, kairomones can be utilized to trap natural enemies (Aldrich et al. 1984, Payne et al. 1984). Before such monitoring can become practical, however, field study is necessary to understand how trap catches relate to population density in a variety of environmental conditions.

CONCLUSIONS

Basic research aimed toward understanding how semiochemicals influence the behavior of natural enemies could lead to the development of practical techniques that would increase the efficacy of biological control by means of behavioral manipulation. In addition to continued basic studies of entomophage behavior, this work should include modeling studies to enable entomologists to predict the effects of semiochemical manipulation (Stimac and O'Neil 1985), and the selection of combinations of natural-enemy species and behavior-modifying chemicals which can consistently aid in pest suppression. This work should be integrated by ecological (Levins and Wilson 1980) and evolutionary (Charnov and Skinner 1985) theory to develop a sound understanding of the interactions between populations of pests and their natural enemies. With a broader understanding of the role of foraging behavior in population dynamics, more reliable techniques for manipulating populations of natural enemies could be developed to achieve effective biological control of *Heliothis* spp.

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Development and Use of Microbial Agents for Control of *Heliothis* spp. in the USA

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ABSTRACT

Although a number of pathogens have been reported from larvae of *Heliothis* spp., only a very few of these have been developed to the point where they can be used as microbial control agents. Efforts in the USA have been concentrated on *Bacillus thuringiensis*, the *Heliothis zea* nuclear polyhedrosis virus, and the fungus, *Nomuraea rileyi*. *B. thuringiensis* is the only microbial agent that is commercially available for control of *Heliothis* spp. However, most pathogens lack the efficacy to compete with chemical pesticides and can only be recommended for suppression of *Heliothis* populations. The *H. zea* NPV has been shown to be an effective control agent of *H. zea* and *H. virescens* and is labeled for use on a number of crops; however, the commercial preparation of the virus is no longer available. *N. rileyi* has shown some promise against several lepidopterous pests on soybeans, including *Heliothis* spp., but commercial development of this material does not appear likely. In general, attempts to replace chemical with microbial insecticides have met with limited success. Acceptance and widespread use of the pathogens currently registered for control of *Heliothis* spp. have yet to materialize, and future efforts should possibly be directed toward alternative approaches for the use of pathogens in pest management systems.

Populations of the corn earworm, *Heliothis zea* (Boddie), and the tobacco budworm, *Heliothis virescens* F., are attacked by a wide variety of naturally occurring pathogens in the USA. Some of these have been recognized as important factors in the suppression of these pests on several major crops. In recent years there has been an increased effort to obtain information on the occurrence of these pathogens, yet their impact on the population dynamics of *Heliothis* spp. is still poorly understood.

Most insect pathogens, like other biological control agents, require a certain level of host density to be able to maintain themselves in a popula-

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tion. Epizootics of these pathogens usually occur when there is a pest outbreak, and in many cases considerable crop damage has been sustained before population levels are suppressed. Thus, the often-heard criticism of pathogens is that their effects on pest populations are usually too little and too late. Since it is unrealistic to expect naturally occurring pathogens to maintain pest populations consistently below economic threshold levels, the question becomes one of manipulating and utilizing them more effectively. Approaches to the use of pathogens for pest population suppression usually fall into one of the following categories:

1. To replace chemical insecticides (inundative approach).
2. To delay use of chemical insecticides for preservation of natural enemies (early-season treatments).
3. To apply pathogens on a limited basis for induction of epizootics (inoculative approach).
4. To introduce pathogens into agroecosystems where they do not occur naturally (classical biological control approach).
5. To enhance development of naturally occurring pathogens by manipulation of the environment (e.g. cultural practices).
6. To aid in control of individual pest species or pest complexes when used in combination with other pesticides (integrated pest management).

Most of the attempted uses of insect pathogens to date fall under category 1, and much of this effort in the USA has been concentrated on a very small number of pathogens. The information presented in this paper on development of microbial agents for control of *Heliothis* spp. is centered around one bacterial species, *Bacillus thuringiensis* Berliner; one viral agent, *Baculovirus heliothis*; and one fungal pathogen, *Nomuraea rileyi* (Farlow) Samson.

In general, attempts to replace chemical with microbial insecticides have met with limited success. Acceptance and widespread use of the pathogens currently registered for control of *Heliothis* spp. have yet to materialize, and future efforts should possibly be directed toward alternative approaches for the use of pathogens in pest management systems.

BACILLUS THURINGIENSIS

The history of the development of *B. thuringiensis* in agroecosystems was recently summarized by Beegle (1979). In the USA, the first commercial formulation was produced in 1957 and was registered for use in 1961. These early formulations (mostly *B. thuringiensis* var. *thuringiensis*) were mainly used on cole crops for control of the cabbage looper, *Trichoplusia ni* (Hübner) and the imported cabbageworm, *Pieris rapae* (L). Due to low strain potency and lack of adequate standardization, performance of these

early formulations was erratic. As a result *B. thuringiensis* was not commonly accepted and received little attention for control of *Heliothis* spp.

A new, more potent strain of *B. thuringiensis* (HD-1) was developed by Dulmage (1970) in the late 1960s. This strain, identified as *B. thuringiensis* var. *kurstaki*, was 20 to 200 times more active than the *B. t.* var. *thuringiensis* strains being used in commercial formulations at that time. The adoption of the HD-1 strain by industry and the development of procedures for standardizing formulations on the basis of potency rather than spore count were major advances in the development of *B. thuringiensis* as an effective microbial insecticide (Dulmage 1973). These developments stimulated considerable research and commercial interest in the use of *B. thuringiensis* for control of *Heliothis* spp. This led to the registration of this material for control of *Heliothis* spp. on cotton, tobacco, soybeans, peanuts, sunflowers, and some vegetable crops. Unfortunately, *H. zea* and *H. virescens* were found to be more resistant to *B. thuringiensis* than most of the other lepidopterous pests which attacked these crops.

On cotton, the new strain was found to be superior to previous formulations (Hopkins and Moore 1983) but control of *Heliothis* spp. was erratic and marginal at best when used at the recommended rates of $4.5–18 \times 10^9$ IU/ha (Bull et al. 1979, Durant 1977, Patti and Carner 1974, Yearian et al. 1980, Yearian and Phillips 1983). McGarr et al. (1970) reported that rates of $48–71 \times 10^9$ IU/ha on a 5-day schedule were necessary to obtain adequate control of *Heliothis* spp. on cotton. At these rates, control of *Heliothis* spp. is not economically practical.

On soybeans, commercial preparations of *B. thuringiensis* have been effective against a number of the soybean Lepidoptera. However, *H. zea* is the least susceptible of all the lepidopterous pests found in soybeans. Ignoffo et al. (1977) testes *B. thuringiensis* against six hosts and found *H. zea* to be the most resistant of the group. The LC_{50} for *H. zea* was three to four times that for *Trichoplusia ni* and 30 times more than for the velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner) and the green cloverworm, *Plathypena scabra* (F.).

Turnipseed (1973) tested *B. thuringiensis* formulations in soybeans and reported some suppression but not control of *H. zea*. Ignoffo et al. (1977) estimated that for effective suppression of *H. zea*, a dosage of 3.8–4.4 kg/ha would be required.

Bacillus thuringiensis is the only currently registered microbial agent that is commercially available for use on soybeans. With the increased costs of development and production of synthetic chemical insecticides, the cost of *B. thuringiensis* on a per application basis compares favorably with many of the chemical insecticides commonly used on soybeans (Beegle 1979, Ignoffo 1979). Strains of *B. thuringiensis* have been tested that are more effective than the HD-1 strain against *H. zea* (Beegle 1979).

Research in this area could result in *B. thuringiensis* preparations that are effective against an increased spectrum of soybean insect pests.

Commercial preparations of *B. thuringiensis* have been used on tobacco for the past 10 to 15 years. Besides being extremely effective in spray applications against the tobacco hornworm, *B. thuringiensis* has also been used successfully in cornmeal bait preparations against the tobacco budworm. Hand-drop bait applications (containing 1–2% *B. thuringiensis*) to the bud area of the young tobacco plants are more effective in controlling *H. virescens* than conventional spray applications of chemical insecticides (Albert Johnson, pers. comm.). Abbott Laboratories has recently developed a new bait formulation of cracked corn containing 10% *B. thuringiensis*, which can be applied in conventional Gandy-type equipment. This would eliminate the necessity for hand applications. Results from recent tests with this new formulation appear promising.

Preparations of *B. thuringiensis* have been tested against *H. zea* on sweetcorn with only limited success (James and Greene 1969, 1972). Staples et al. (1968) reported that *B. thuringiensis* was completely ineffective against *H. zea* when 11 applications of 2.24 kg/ha were made to sweetcorn in Nebraska. Due to the necessity for high levels of control in this high-value crop, *B. thuringiensis* has not been recommended for use on sweetcorn.

In general, *B. thuringiensis* has proven to be only moderately effective for control of *Heliothis* spp. on most crops. Because of its positive attributes—such as host specificity, safety, availability, and ease of application—interest in its use in pest management systems has persisted. As a result, efforts are being made to improve the efficacy to acceptable levels. These efforts have involved selection of more virulent strains, development of spray adjuvants, and combinations with chemical insecticides and other pathogens.

Altogether, 317 isolates of *B. thuringiensis* have been screened for activity against *H. virescens* (Beegle 1983). Three isolates with approximately three to five times greater activity than the HD-1 strain were selected for field tests. One isolate (HD-263) was found to be superior but was somewhat erratic in further tests comparing it with HD-1 strain.

Sandoz Inc. has recently released a new formulation of *B. thuringiensis* (Javelin®) for field testing. Tests during 1985 have shown somewhat increased activity against *Heliothis* spp. than their Thuricide® (HD-1) formulation.

A number of gustatory adjuvants, some of which provide a degree of sunlight protection, have been tested and have frequently resulted in improved field efficacy of *B. thuringiensis* (Bell and Romine 1980, Hopkins and Moore 1983, Watson 1983). In general the more complex adjuvants, eg. Coax ®(Trader's Oil Mill) and Gustol® (Sandoz Inc.) have been

most effective. In laboratory studies, these resulted in a 10- to 20-fold increase in *Heliothis* spp. mortality when used in combination with *B. thuringiensis* (Smith and Hostetter 1982). These adjuvants appear to alter feeding behavior of *Heliothis* spp. larvae, which results in increased consumption of the microbial agent (Luttrell et al. 1983).

Bacillus thuringiensis has also been tested in combination with reduced rates of insecticides. Hopkins and Moore (1983) conducted a series of tests of *B. thuringiensis*-insecticide combinations with variable results. They found that the relative performance of the combinations depended on pest population pressure, weather conditions, and use of gustatory adjuvants. The most promising results have been obtained with combinations of *B. thuringiensis* and the ovicide, chlordimeform (Blythe 1981, Yearian et al. 1980).

VIRUSES

A number of viruses have been reported from larvae of *Heliothis* spp., including several nuclear polyhedrosis viruses (NPV), a cytoplasmic polyhedrosis virus, a granulosis virus, an iridovirus, and an unidentified spindle-shaped virus (Smith 1967, Stadelbacher et al. 1978, Carner and Hudson 1983). However, the NPVs are the only viruses that have shown promise for use as microbial insecticides, and the *H. zea* NPV is the only *Heliothis* virus registered for use in the USA.

Heliothis zea Nuclear Polyhedrosis Virus

The early development of *H. zea* NPV was for control of *H. zea* and *H. virescens* on cotton. The impetus for development of this virus was provided by the work of Ignoffo and coworkers in the early 1960's (Ignoffo 1973). Results of early field tests with *H. zea* NPV on cotton were erratic. In 1963, virus treatments at 247 LE/ha gave control comparable to that of standard insecticides (Ignoffo et al. 1965), but in a similar test in 1964 the virus did not provide satisfactory protection (McGarr and Ignoffo 1966). In a series of tests from 1964 to 1966 by Montoya et al. (1966) and McGarr (1968), virus treatments consistently resulted in increased cotton yields over the untreated control, but less than the chemical insecticide standard. A rate response was evident, with increased virus concentration resulting in increased cotton yields.

Test results were sufficiently promising for industry to begin development of the *H. zea* NPV in 1966. However, field performance of the commercial products continued to be inconsistent. Because of this inconsistency, the inability to compete with chemical insecticides, particularly at high *Heliothis* population levels, and uncertainties concerning the

safety requirements for registration, commercial and research interest in *Heliothis* NPV dwindled in the late 1960s and early 1970s (Yearian and Young 1982). One of the original producers of the virus (Nutrilite Products Inc.) withdrew from active research and development and in 1973 Sandoz Inc. purchased the Biological Pesticides Division of the International Minerals and Chemicals Corp., including the *H. zea* NPV. Sandoz Inc. developed new virus formulations with improved shelf life and greater activity (Ignoffo et al. 1976). After additional field-testing in 1975, one of the formulations, SAN 240 WP, was registered under the trade name Elcar prior to the 1976 growing season.

Results of subsequent field tests with Elcar® have shown a consistent improvement in efficacy. However, at moderate to high *Heliothis* population levels the virus has been less effective than standard insecticide treatments (Bull et al. 1979, Luttrell and Yearian 1981, Pfrimmer 1979, Stacey et al. 1977, Yearian et al. 1980).

Like *B. thuringiensis, H. zea* NPV alone for control of *Heliothis* spp. on cotton has not been commonly accepted (Yearian and Young 1982). An alternative approach to the use of NPV on cotton has been in areawide *Heliothis* management programs: the virus is applied early in the season over the entire cotton acreage in the management area to reduce *Heliothis* populations and prevent occurrence of economically damaging infestations later in the growing season (Phillips et al. 1979).

Results of a 1977 areawide program in Arkansas using *H. zea* NPV were most encouraging (Phillips et al. 1981). In general, only one additional insecticide treatment was required in the management area for the remainder of the season. Tests during subsequent years (1978–1982), however, have raised questions concerning the feasibility of these areawide programs. These include (1) the increased level of *Heliothis* population present in soybeans following wheat in late June and early July, (2) the resurgence of the boll weevil as a consistent, serious pest, and (3) failure of the programs to operate successfully without direct input by research personnel (Yearian and Phillips 1983).

Efforts similar to those described for *B. thuringiensis* have been made to improve the efficacy of formulations of the *H. zea* NPV. Although selection of improved strains has not received much attention, there appears to be some potential for developing a more virulent strain than the one being used currently. Shapiro and Ignoffo (1970) examined the activity of 34 isolates of the virus. They found that activity varied 56-fold, based on laboratory LD_{50} values. Spray adjuvants similar to those used with *B. thuringiensis* have also been used successfully to improve the efficacy of the *H. zea* NPV. Coax® and Gustol® were the most effective adjuvants. In field tests with combinations of microbial agents and chemical insecticides, the *H. zea* NPV was found more effective than the *B. thuringiensis* in combinations with chlordimeform (Yearian et al. 1980).

Although the *H. zea* NPV was originally developed for use on cotton, it has been tested for efficacy on a number of other crops. On soybeans, Ignoffo et al. (1978) compared the virus with *B. thuringiensis*, and with the fungus, *Nomuraea rileyi*, against caged *H. zea* larvae and found the virus to be the most effective of the three in the suppression of feeding by the larvae. Luttrell et al. (1982) found that treatments with the commercial formulation, Elcar®, caused significantly higher mortality (88–98%) in soybeans than in cotton. This may be because *H. zea* is exposed during its entire larval stage, and spray coverage can be much more effective than on cotton.

The *H. zea* NPV has been tested on corn with some success (Tanada and Reiner 1962, Hamm and Young 1971). Of the microbial agents available, the NPV appears to have the most potential due to its ability to kill small larvae before they cause damage and its greater potential for causing epizootics.

Elcar® has been tested against budworms on tobacco with some success, but, because of its delayed activity, the virus has not been as effective as *B. thuringiensis*; larvae can cause extensive damage to the buds before they are killed by the virus (Albert Johnson, pers. comm.).

In 1982 Elcar®, which had previously been registered only for use on cotton, was granted a broad-label expansion and was labeled for use on sorghum, soybean, tomatoes, corn, tobacco, peanuts, lettuce, strawberries, and beans. However, this expansion in the label came at the time when the newly developed pyrethroids became available for highly effective control of *Heliothis* spp. on many of these same crops and the demand for Elcar® was drastically reduced; thus Sandoz ceased commercial production of the virus in 1984.

Other Nuclear Polyhedrosis Viruses

A nuclear polyhedrosis virus of the alfalfa looper, *Autographa californica* (Speyer) has been shown to infect a number of species of Lepidoptera, including *H. zea* and *H. virescens* (Vail and Jay 1973, Vail et al. 1978). An experimental formulation produced by Sandoz (SAN 440 WP) was field-tested on cotton from 1977 to 1979. The virus was efficacious but inferior to *H. zea* NPV in most tests (Pfrimmer 1979). In tests on soybeans, the *Autographa* NPV was not effective in reducing numbers of *Heliothis* spp. (Brooks and Sprenkel unpubl., Yearian unpubl.). The unfavorable performance of this virus was probably due to its low level of virulence against *H. zea* larvae (Vail et al. 1978). *Heliothis* populations in most field tests in cotton were mixtures of *H. zea* and *H. virescens*, and in soybeans, mostly *H. zea*.

Nuclear polyhedrosis viruses isolated from *Heliothis armigera* (Hübner) have also been tested. The efficacy of an isolate from the USSR

was comparable, but not superior, to *H. zea* NPV in tests in Arkansas (Yearian and Young 1982).

FUNGI

Fungal pathogens that are known to infect larvae of *Heliothis* spp. include the imperfect fungi, *Beauveria bassiana* and *Nomuraea rileyi*, and at least two species of the family Entomophthoraceae. Some of these fungi are important in the natural regulation of *Heliothis* spp. populations on certain crops. Natural epizootics of *Entomophaga* (= *Entomophthora*) *aulicae* were observed causing 48 to 100% mortality in *H. zea* larvae on sorghum (Hamm 1980). *E. aulicae* and an unidentified species of *Erynia* cause significant reductions in late-season *H. zea* populations in soybeans (Carner unpubl.). *N. rileyi*, however, is the most widespread of the fungi reported from *Heliothis* spp. and is the only fungal pathogen which has been studied extensively as a potential microbial control agent of *Heliothis*.

Nomuraea rileyi

Although *N. rileyi* has been reported from several crops, it has mainly been studied in relation to its occurrence in lepidopterous pests of soybeans. It has been reported from all of the major soybean-producing areas of the USA and appears to be worldwide in its distribution (Carner 1980). In most areas where it occurs, it is the most abundant pathogen affecting the insect pest complex. Its widespread occurrence and relative abundance are probably due to its wide host range, which includes all of the major lepidopterous pests of soybeans (Puttler et al. 1976).

Studies in North Carolina and Missouri have shown that *N. rileyi* may have potential for use as a microbial insecticide. Sprenkel and Brooks (1975) applied *Nomuraea*-killed *H. virescens* cadavers, cut into 3-mm sections, to soybean plots and were able to induce an epizootic of the fungus 14 days earlier than that which occurred in the untreated plots. Populations of *H. zea* and pod damage in treated plots were significantly lower than in untreated plots. Ignoffo et al. (1976) were also able to initiate epizootics of *N. rileyi* 14 days early with one application of a conidial suspension.

An areawide test was initiated by Ignoffo in 1982 to test the efficacy of spore preparations of *N. rileyi* as prophylactic treatments and as treatments for short-term control. An experimental formulation of *N. rileyi* spores was produced by Abbott Laboratories and was distributed to researchers throughout the southeastern USA. Results have been variable, but in locations with adequate lepidopterous hosts susceptible to the

strains used and when favorable environmental conditions occurred, epizootics were successfully initiated after prophylactic applications of spore powder. Treatments for short-term control generally did not meet with success.

SUMMARY AND CONCLUSIONS

Because of their unique properties of specificity, safety, and biodegradation, microbial insecticides are an attractive alternative to chemical insecticides in insect pest management systems. However, the development and use of these microbial agents for pest control in agricultural situations has not progressed as rapidly as anticipated. Despite extensive research efforts by government agencies and industry, the acceptance and widespread use of entomopathogens have yet to materialize.

Although *B. thuringiensis* is labeled for use against *Heliothis* spp. on a number of crops, it lacks the efficacy to compete with chemical insecticides. At present it can only be recommended as a suppressant rather than a control agent for *Heliothis*. Its future potential will depend on whether new formulations and/or strains of *B. thuringiensis* with improved efficacy against *Heliothis* spp. can be developed.

The *H. zea* NPV, although still labeled for use on a number of crops, is no longer commercially available. In this case the major limiting factor appears to be economic. The host specificity of baculoviruses that makes them highly desirable for use in IPM systems could be the major deterrent to their commercial development. Evaluations of these materials in IPM systems requires substantial investments in time and materials. With host-specific materials such as viruses, the market potential is limited for most pest species, and possibilities for recovery of a return on investments are not financially attractive (Yearian and Young 1982). Prospects for renewed industrial interest in development and commercialization of microbial insecticides do not appear good. Thus, chances of having new materials available in the future appear minimal.

The use of highly specific pesticides, such as microbials, is very appealing from an ecological or environmental standpoint, but unfortunately, not from an economic standpoint. Neither industry nor growers appear interested in the development of host-specific pesticides. With current attitudes, it is doubtful that development of microbial insecticides will be expanded unless means for overcoming the economic disadvantages are developed. Economic incentives or direct involvement of the public sector may be needed (Yearian and Young 1982).

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Development and Use of Microbial Agents for Control of *Heliothis* spp. (Lep.: Noctuidae) in India

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ABSTRACT

Native pathogens of *Heliothis armigera* (Hübner) reported from India include nuclear polyhedrosis virus, cytoplasmic polyhedrosis virus, granulosis virus, *Bacillus thuringiensis* Berliner, *Beauveria bassiana* (Balsamo), *B. brongniartii* (Sacc.), *Metarhizium anisopliae* (Metschnikoff), *Nosema* sp., *Vairimorpha* sp., and *Ovomermis albicans* (Sieb). Of these, the nuclear polyhedrosis virus (NPV) has been the most extensively studied for its morphology, dissolution, and haemagglutination characteristics, pathogenicity, persistence in soil and foliage, mass production, safety and field efficacy in the control of the pest on chickpea, pigeonpea, field bean, cotton, sunflower, and tomato.

Three to four sprays of NPV of 250 to 375 LE (larval equivalents)/ha (1 LE = 6 × 10⁹ PIB) were found to give good control of *H. armigera*, particularly on chickpea. Crude sugar 0.5%, groundnut oil cake 1%, chickpea flour 1%, or a combination of crude sugar 0.25% + chickpea flour 0.25% + groundnut oil cake 0.5% were found to increase NPV-caused insect mortality by 40 to 60% on chickpea. Application of NPV along with insecticides or application of virus followed by insecticide spray 3 to 5 days later resulted in better control of the pest on chickpea, pigeonpea, cotton, and sunflower.

Dosage-mortality response studies have shown that virus infection increased the susceptibility of larvae to insecticides. Though virus infection suppressed the parasitization of larvae by *Campoletis chlorideae* Uchida in the laboratory, there was no marked effect on the incidence of the parasitoids *C. chlorideae* and *Eucelatoria* sp. in the NPV-treated plots. These parasitoids could transmit the virus to host larvae by oviposition or larviposition. The virus did not produce any deleterious effects on the species of parasitoids, predators, albino rats, poultry birds, and fish tested.

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Cross-infectivity studies have shown that *H. armigera* was highly susceptible to NPV of *Adisura atkinsoni* Moore.

B. thuringiensis—as Bactospeine, Thuricide, or Dipel—was also effective against *H. armigera* on chickpea.

Of the different species of *Heliothis* occurring in India, *Heliothis armigera* (Hübner) is the most widely prevalent and devastating pest, with an extensive host range, causing severe damage to many food and fiber crops (Anon. 1977). The damage due to *H. armigera* is particularly severe on chickpea and pigeonpea in the Indian subcontinent, where 80% of the world's chickpea and 90% of the world's pigeonpea crops are grown (Bhatnagar et al. 1982). An average infestation of one·larva per plant of pigeonpea can cause a yield loss of 1015 kg/ha (Reddy and Channa Basavanna 1978). In sorghum, yield losses of 18 to 26% have been reported (Rawat et al. 1970); in cotton, 41 to 56% (Kaushik et al. 1969). In tomato the damage caused may range from 40 to 50% (Srinivasan 1959).

In view of the high cost of chemical pesticides and the increasing awareness of pesticide residues in food, there is growing interest in the use of natural enemies for the management of *Heliothis*. Jayaraj (1985a) has reviewed the literature on the utilization of NPV for *H. armigera* control in India. This paper reviews attempts made to identify naturally occurring pathogenic microorganisms and studies leading to the development and evaluation of the most promising ones for the control of the pest. *H. armigera* being the predominant species, all the attempts made so far concern the testing of microbial agents against this species only.

PATHOGENIC MICROBES REPORTED FROM INDIA

Of the native pathogens of *H. armigera* (Table 1), the nuclear polyhedrosis virus (NPV) has been the most extensively studied for its pathogenicity, mass production, safety, and field efficacy in controlling the pest of chickpea, pigeonpea, field bean, sunflower, cotton, and tomato. Attempts have also been made to utilize *B. thuringiensis* to control *H. armigera* on crops like chickpea, field bean, pigeonpea, and tomato, which are discussed elsewhere in this paper. No attempts have been made to study the control potential of other pathogens.

Nuclear Polyhedrosis Virus

The occurrence of nuclear polyhedrosis virus in *H. armigera* in India was first reported by Patel et al. (1968) in Gujarat. In Tamil Nadu, Jacob and Subramanian (1972) described the polyhedra of *H. armigera* NPV to be irregular in shape, the diameter ranging from 0.5 to 1.4 μ with an average

Table 1. Microbial pathogens of Heliothis spp. reported from India

Pathogen	Reference
Viruses	
Nuclear polyhedrosis virus (NPV)	Patel et al. (1968)
Cytoplasmic polyhedrosis virus (CPV)	Rabindra and Subramanian (1973a)
Granulosis virus (GV)	Narayanan (1985a)
Bacteria	
Bacillus thuringiensis Berliner	Majumdar et al. (1955)
Fungi	
Beauveria bassiana Balsamo	Jayaramaiah (1981)
B. brongniartii (Sacc.)	Jayaramaiah (1981)
Metarhizium anisopliae (Metschnikoff)	Urs and Govindu (1971)
Protozoa	
Nosema sp.	Anon. (1985)
Vairimorpha sp.	Narayanan (1985b)
Nematodes	
Ovomermis albicans (Sieb.)	Bhatnagar et al. (1982)

of 0.89 ±0.012 μ. The virions were occluded singly. Rabindra (1973) found that the diameter of the polyhedra varied from 0.71 to 2.21 μ with an average of 1.31 ± 0.03 μ. The carbon replicas did not show any surface patterns.

The factors responsible for the dissolution of polyhedral inclusion bodies of *H. armigera* NPV were studied by Narayanan (1979), who examined the role of silicon, magnesium, and iron in the skeletal lattice framework of polyhedra and the influence of alkaline components, pH, and proteolytic enzymes of the insect host on the dissolution of the polyhedra.

Narayanan (1985c) has studied the invasive mechanism of NPV of *H. armigera* through a haemagglutination technique and found that it has more or less the same mechanism of adsorption of viruses to erythrocytes mediated to the same receptors as vertebrate viruses. Thus, it is possible by the haemagglutination technique to detect and monitor the virus in the environment.

Studies on the susceptibility of the different larval instars revealed that the earlier instars were very highly susceptible to the virus (Rabindra and Subramanian 1974) and the LT_{50} was shorter in younger larvae than in older ones (Narayanan 1979). These findings indicate that for successful control of the pest, the application of the virus should coincide with the occurrence of early-stage larvae in the field. The virus was found to infect the nuclei of fat body, hypodermis, tracheal matrix, haemocytes, nerve cells of ganglion and brain, foregut, connective tissues surrounding the midgut, silk glands, and epithelium of the gonads (Rabindra and Subramanian 1974). Growth parameters such as consumption index, growth

rate, approximate digestibility, gross efficiency of ingested food to the body substance, and net efficiency of digested food to the body substance were lower in NPV-infected larvae than in healthy ones. The changes in biochemical constituents in the larvae due to NPV infection and the possible mode of action of NPV have been discussed by Narayanan (1979).

Comparison of NPV isolated from different locations

Odak et al. (1982) found considerable difference in infectivity of NPV isolated from different locations. The culture isolated locally from Narasinghpur gave a higher mortality (93.3%) than cultures from the other centers.

Persistence of virus in soil and on foliage

Adsorption of the polyhedra in two types of soils was studied by Narayanan et al. (1985). It was found that the adsorption rate was higher in Alfisols (0.88) than in Vertisols (0.69). The activity of NPV on tomato leaves steadily decreased with increasing time of field exposure (Anon. 1985); 4 days after exposure, activity was only 36.7% of the original, and by the tenth day it was as low as 6.4%. This finding stresses the need to use suitable UV protectants along with the virus.

Effect of host plants

When NPV was applied to flowers and pods of several host plants, the mortality of fourth-instar larvae was significantly higher in larvae on pods of chickpea and pigeonpea than on the flowers and fruiting parts of other plants. The mortality was minimum on field bean flowers (Vijayakumar 1980). This is probably due to the differential concentration of polyhedra on the different plant parts and/or differential feeding preference of the insect on the various plant parts. The efficacy of the virus could be increased by the use of proper surfactants. When reared from the first instar on chickpea, sunflower, bean, and pea, larvae showed a higher percentage of NPV-caused mortality on pea and sunflower than on bean and chickpea (Pawar et al. 1981). However, further studies are necessary on the influence of host plants.

Increasing the effectiveness of NPV

Rabindra and Jayaraj (1985a) conducted a series of pot culture experiments to identify suitable adjuvants which could be cheap and easily available. Fifteen 20- to 25-day-old chickpea plants were sprayed with 10 ml suspensions of different treatments containing the virus and adjuvants. Spraying was done with a hand atomizer, and the pots were rotated for uniform coverage. After drying, 15 to 25 early second-instar larvae of *H. armigera* of uniform age were released on the plants and allowed to feed for 18 to 24 h. They were then transferred to individual vials containing diet

(lacking formalin) and the percent mortality was recorded on the seventh day.

In the first experiment, addition of crude sugar of sugarcane 0.5% was found to give increased mortality from NPV. This might be due to the phagostimulant action of crude sugar. In the subsequent two experiments, the efficacy of crude sugar of sugarcane was compared with those of coconut and palmyrah, along with other adjuvants like cane sugar (sucrose), groundnut oil, and cotton seed oil. All three kinds of crude sugar significantly increased NPV-caused mortality over NPV alone; crude sugar of sugarcane increased it the most.

In the fourth experiment, the efficacy of different oilcakes and flours was compared with that of crude sugar. Groundnut oilcake 3% and chickpea flour 1% were found to be as good as crude sugar. Because of the high cost of applying groundnut oilcake at 3%, the efficacy of the cake at 1% was compared with crude sugar 0.5% and with a combination of crude sugar, oilcake, chickpea flour, and cottonseed oil. Groundnut oilcake 1% was found to be as effective as crude sugar 0.5% but a combination of crude sugar 0.25% + chickpea flour 0.5% + groundnut oilcake 0.5% was found to give significantly higher percent mortality than crude sugar 0.5%. Roome (1975) has reported that addition of molasses 0.6% greatly improved the performance of NPV in the field against *H. armigera* larvae on sorghum and cotton. We have tried crude sugar, since molasses is not easily available to farmers, whereas crude sugar is.

These encouraging results indicate clearly the possibility of using such adjuvants as crude sugar or groundnut oilcake—which are both cheap and easily available to the Indian farmer and which possess the required properties for an adjuvant as described by Bell and Kanavel (1978)—to obtain better control of *H. armigera*, especially on chickpea.

Further experiments are in progress to study the performance of these materials in the field as spray adjuvants for NPV and we are hopeful of getting positive results. Experiments are also in progress to study the stability of NPV when stored in crude sugar.

NPV infection and insecticide susceptibility

Nuclear polyhedrosis virus infection in *H. armigera* increased the larval susceptibility to insecticides. When fifth-instar larvae were exposed to a dose of 315 PIB/mm^2 of diet surface, the susceptibility to endosulfan, fenvalerate, cypermethrin, and chlorpyriphos increased several fold (Srinivas 1985). It is suspected that *H. armigera* populations may have developed resistance to some of the pesticides used against them. Entomopathogens; when properly introduced into the population, can break such insecticide resistance (Listov and Nesterov 1976, Rabindra and Jayaraj 1985b, Rud and Bellonick 1984).

The NPV-induced susceptibility of larvae to insecticides may be the possible reason for the superior control achieved by application of NPV followed by endosulfan 3 and 5 days later on sunflower and chickpea, respectively, as discussed elsewhere in the paper.

Field trials

In all the field experiments conducted to evaluate the virus against *H. armigera*, only native NPV was used in the form of semipurified polyhedral suspension. No commercial NPV formulation like Elcar is available in India. The virus was tried at doses ranging from 125 to 375 LE/ha, either alone or in combination with organophosphorus, organochlorine or synthetic pyrethroid insecticides.

Chickpea

The results of field trials with NPV on chickpea have been very promising (Jayaraj 1985b), probably because young larvae feed on the leaflets, scraping the epidermal tissues, and the older larvae feed on the leaves, flower buds, and pods of chickpea. When larvae feed on the foliage, they acquire the virus better than when they feed on the flowers or pods.

Narayanan (1979) conducted two field experiments. The efficacy of three sprays of NPV at 125 and 250 LE/ha was compared with that of a single application of endosulfan 0.07% by high volume application. The virus was applied in the evening hours along with Triton × 100 at 0.01% as wetting agent.

The larval population was significantly reduced in virus treatments when compared with the control. The virus treatments reduced leaflet damage considerably and were as effective as endosulfan. The damage to flowers and pods was significantly lower than with endosulfan. Both total grain yield and number of pods formed were maximum in plots treated with NPV at 250 LE/ha.

In a second experiment, the virus was applied in the morning hours along with an adjuvant, which was a liquid flow material formulated by Sandoz-Wander, Inc., at 10% spray fluid concentration with inclusion of 2.5% cane sugar. It was reported that application of three rounds of NPV at 250 LE/ha plus adjuvants effectively checked larval population; reduced damage to leaflets, flowers, and pods; and increased total number of pods formed and yield (Table 2). Reduction of pod damage in chickpea due to application of NPV has also been reported by Makode (1978), Bakwad (1979), Santharam and Balasubramanian (1982), Mistry et al. (1984) and Rabindra and Jayaraj (1985c). Application of NPV at 375 LE/ha was found to reduce pod damage and was comparable to carbaryl (Santharam and Balasubramanian 1982). Rabindra and Jayaraj (1985c) found that application of NPV at 250 LE/ha, followed by endosul-

Table 2. Effect of field application of NPV and endosulfan on H. armigera larval population, damage, and yield in chickpea[1]

Treatment[2]	Larvae/10 plants after 7 days	Mean % damage in			Healthy pods/ plant	Yield (kg/ha)
		Leaflets	Flowers	Pods		
Evening application						
NPV 250 LE/ha	1.6[a]	0.41[a]	5.68[a]	6.51[a]	372.6[a]	696[a]
NPV 125 LE/ha	3.8[b]	0.67[a]	4.10[a]	8.87[a]	305.4[a]	643[a]
Endosulfan 525 g ai/ha	1.0[a]	0.25[a]	35.04[b]	22.80[b]	351.4[a]	660[a]
Control	14.2[c]	2.50[b]	51.26[b]	48.65[c]	163.8[b]	378[b]
Morning application						
NPV 250 LE/ha + adjuvant[3]	1.6[a]	0.45[a]	8.0[a]	2.3[a]	158.0[a]	1089[a]
NPV 250 LE/ha	3.6[b]	2.23[b]	14.5[b]	10.2[b]	84.8[b]	583[b]
Endosulfan 525 g ai/ha	1.2[a]	0.45[a]	31.4[c]	28.8[c]	90.0[b]	571[b]
Control	8.2[c]	3.18[b]	44.5[d]	48.7[d]	54.4[c]	372[c]

Source: Narayanan (1979).

[1]In a column, means followed by similar letters are not different (P = 0.05) by Duncan's Multiple Range Test.

[2]NPV and NPV + adjuvant, three sprays at weekly intervals; endosulfan single application.

[3]Liquid flow material formulated by Sandoz-Wander, Inc., at 10% spray fluid concentration with 2.5% cane sugar.

fan 262 g ai/ha 5 days later, reduced larval population and pod damage better than either treatment alone.

Application of a chemical pesticide following virus application is a sound approach: excellent control can be achieved when the larvae are weakened by viral infection. This method also permits optimal application of pesticides, to conserve parasitoids and predators.

Application of a mixture of virus + insecticide has also been reported to give better control than either applied alone; NPV at 125 LE/ha + endosulfan 0.035% spray with high volume knapsack sprayer in the evening hours reduced pod damage significantly. The pod damage in plots receiving NPV spray @ 250 LE/ha was 14.0%, whereas it was only 3.7% in plots treated with a mixture of NPV 125 LE/ha + endosulfan 0.035%. Untreated plots recorded 21.4% pod damage (Jayaraj and Santharam, unpublished). Mistry et al. (1984) studied the field efficacy of NPV at two locations and found that application of five rounds of NPV at 250 LE/ha at weekly intervals could reduce the larval population as well as damage to pods.

H. armigera is the only serious pest damaging chickpea and the prospects for successfully controlling it with NPV are very promising. There is good scope for integrating the use of NPV with other biological control

factors, such as parasitoids, and optimal and selective pesticide application to manage the pest with least hazard to the ecosystem.

Pigeonpea

H. armigera causes severe yield loss on pigeonpea by feeding on the flowers and seeds in pods. The efficacy of NPV for its control was studied in several field experiments (Vijayakumar 1980; Santharam et al. 1981; Anon. 1985; Srinivas 1985; Sithanantham pers. comm.).

Application of NPV 250 LE/ha + endosulfan 0.07% was reported to give better control of the pest than application of NPV at 250 LE/ha alone. However, this was in no way superior to application of endosulfan 0.07% alone. Hence, we may not derive much benefit out of such a combination on pigeonpea. The control achieved by NPV application on rainfed pigeonpea was equal to that of BHC 10% dust at 25 kg/ha but inferior to endosulfan 4% dust (Vijayakumar 1980).

Though Santharam et al. (1981) could obtain significant mortality of larvae by applying NPV at 375 LE/ha in pot culture studies, appreciable control could not be achieved in the field. Observations on pod damage in experiments at five locations—Madurai, Coimbatore, Ludhiana, Bangalore, and Hyderabad—have shown that application of NPV at 250 LE/ha + endosulfan 0.035% could result in better control of pod damage than application of virus alone (Table 3).

Table 3. Efficacy of NPV on Heliothis armigera *on pigeonpea at five locations in India*

Treatment	Mean % pod damage[1]				
	Madurai	Coimbatore	Bangalore	Ludhiana	Hyderabad
NPV 250 LE/ha	9.8[b]	33.3[b]	24.1[b]	30.4[b]	15.4[b]
NPV 250 LE/ha + endosulfan 0.035%	–	24.5[a]	15.4[a]	20.5[a]	7.4[a]
NPV 125 LE/ha + endosulfan 0.035%	9.1[b]	–	–	–	–
Endosulfan 0.07%	6.0[a]	24.4[a]	15.4[a]	19.6[a]	7.7[a]
Control	19.1[c]	51.6[c]	28.5[c]	25.3[b]	38.8[c]

Sources: Vijayakumar (1980); Anon. (1985); Sithanantham, pers. comm.

[1] In a column, means followed by the same letters are not different statistically (P = 0.05) by LSD.

As on chickpea, spraying a mixture of NPV + endosulfan 0.035% on pigeonpea seems to work better than either treatment alone. Insecticides like chlorpyriphos and cypermethrin were also found to effect good control of *H. armigera* when applied along with NPV. It would be worthwhile to take up detailed studies to fix the optimum levels of virus as well as

insecticides for developing a sound IPM system for chickpea, pigeonpea, and other crops on which the pest occurs.

One major constraint to the successful use of NPV on pigeonpea is the occurrence of insects other than *H. armigera* on the pods. The pod fly, *Melanagromyza obtusa* (Malloch), the plume moth, *Exelastes atomosa* Walker, and the shoot and flower webber, *Maruca testulalis* Geyer, also cause considerable damage to the flowers and pods of pigeonpea. The NPV of *H. armigera* is not infective to any of these insects (unpublished data). However, across most of north India during the *kharif* (rainy) season, the predominant pest is *H. armigera*; thus the use of a species-specific biocontrol agent such as NPV holds great promise.

Field bean

The field bean pod is attacked primarily by *H. armigera, Adisura atkinsoni* Moore, and *Sphaenarches anisodactylus* Walker. NPV has been tested for the control of *H. armigera* as well as *A. atkinsoni.* The NPV of *A. atkinsoni* is also infective to *H. armigera*, which considerably broadens the scope for using NPV to control both borers. Srinivas (1985) observed the effect of NPV of *H. armigera* on pod and seed damage as well as yield. NPV at 125 LE/ha + cypermethrin 0.006% was found to be better than application of NPV alone at 250 LE/ha in reducing damage and increasing yield. Similarly, Jayaraj and Santharam (unpublished) found that a combination of NPV 125 LE/ha + endosulfan 0.035% applied twice with an interval of 1 week, gave appreciable protection of pods against *H. armigera.*

Spraying of NPV of *A. atkinsoni* at 250 LE/ha three times at weekly intervals has been found to effectively control both *H. armigera* and *A. atkinsoni* (Narayanan, unpublished).

Sunflower

Successful control of *H. armigera* on sunflower was demonstrated by Rabindra (1985), using a hand atomizer to apply the virus on the flower heads. A single application of virus at 250 LE/ha followed by endosulfan 0.035% 3 days later was found to be as good as two applications of virus at 250 LE/ha. Observations on the 13th day showed that the virus treatments were more persistent than endosulfan.

Cotton

Work on the use of NPV for the control of *H. armigera* on cotton is rather limited. Vijayakumar (1980) in preliminary field experiments studied the efficacy of NPV applied at different doses with and without UV protectants. The performance of NPV-insecticide mixtures was also investigated. As in chickpea and pigeonpea, a combination of NPV 125 LE/ha + endosulfan 0.035% applied by high volume sprayer was found to be the best, recording minimum damage to squares and bolls (Table 4).

Table 4. Use of NPV and insecticides in the control of field populations of H. armigera on cotton

Treatment	Mean % damage[1]	
	Squares	Bolls
NPV 250 LE/ha	4.04[b]	2.13[a]
NPV 250 LE/ha + skim milk powder 2%	3.64[b]	1.80[a]
NPV 250 LE/ha + starch 2%	3.87[b]	2.17[a]
Monocrotophos 0.025% + NPV 125 LE/ha	3.07[b]	1.38[a]
Endosulfan 0.035% + NPV 125 LE/ha	2.37[a]	1.03[a]
Monocrotophos 0.05%	3.44[b]	1.44[a]
Endosulfan 0.07%	2.44[a]	1.35[a]
Control	9.90[c]	5.80[b]

Source: Vijayakumar (1980).

[1]In a column, means followed by the same letters are not different statistically (P = 0.05) by LSD.

In India, cotton suffers damage by a complex of lepidopterous insects, of which *H. armigera* is just one. We need to identify a virus like that of *Autographa californica* Speyer, with infectivity to at least the most serious pests such as the pink bollworm, *Pectinophora gossypiella* Saunders; spotted bollworms, *Earias* spp.; and the leaf caterpillar, *Spodoptera litura* (F.). Research could also be intensified on the formulation of a bait containing NPV-insecticide mixture to tackle the pest complex on cotton.

Tomato

The work on tomato again is very meager. Mistry et al. (1984) reported that even a low dose of NPV, 100 LE/ha could cause high mortality in *H. armigera* larvae (Table 5). The 35.2% mortality recorded in the control plot in the first trial indicates a high level of natural incidence of virus and/or migration of infected larvae. The impact of virus application is more pronounced in the second trial. More studies are required to evaluate the performance of the virus on tomato for control of *H. armigera*.

NPV × parasitoid interaction

Studies on the interaction between the NPV infection and parasitism

Table 5. Efficacy of NPV for Heliothis armigera control on tomato

Treatment	Trial I		Trial II		
	Mean % mortality	Larvae/ plant	Mean % mortality	Larvae/ plant	Mean % fruit damage
NPV 100 LE/ha[1]	94.5	0.65	80.61	0.08	4.3
Control	35.2	1.94	1.14	0.30	15.6

Source: Mistry et al. (1984).

[1]Five applications at weekly intervals.

by *Eucelatoria* sp. nr. *armigera* Coq. have shown that NPV infection in *H. armigera* larvae did not affect the development of the parasitoid. Maggot development, adult emergence, sex ratio, longevity, and larviposition behavior of adult flies emerging from diseased host larvae were normal (Narayanan 1980). But NPV infection in *H. armigera* larvae suppressed development of *Campoletis chlorideae* Uchida as reported by Odak et al. (1982). However, preliminary field observations on the percentage parasitism by *C. chlorideae* on *H. armigera* in NPV-treated plots suggested that there was no adverse effect of virus application on the development of the parasitoid either in the larval or in the pupal stage (Anon. 1983).

Transmission of NPV by parasitoids

C. chlorideae transmitted the virus to *H. armigera* larvae directly by oviposition, causing 100% mortality (Odak et al. 1982). Studies of the ability of *Eucelatoria* sp. nr. *armigera* to transmit the virus during larviposition revealed the successful transmission of the pathogen (Narayanan 1980). Surveys of natural enemies of *H. armigera* in south-central India have so far revealed 27 species of insect parasitoids (Bhatnagar et al. 1982) and it would be worthwhile to study the promising ones for their ability to transmit the virus to *H. armigera* larvae.

Safety of NPV to nontarget organisms

The NPV of *H. armigera* was tested against 12 species of parasitoids, four species of predatory insects, and one species of predatory mite and was found to be safe to all of them. The virus was also found to be nonpathogenic to the silkworms, *Bombyx mori* L. and *Philosamia ricini* Boisduval (Anon. 1983).

Srinivas (1985) found the NPV to be safe to the parasitoids *Apanteles* sp., *Bracon greeni* Ashmead, *B. hebetor* Say., *Chelonus blackburni* (Cameron), *Eriborus* sp., *C. chlorideae*, and *Eucelatoria bryani* Sabrosky. In preliminary studies, oral administration of the NPV of *H. armigera* produced no deleterious effects on albino rats, white leghorn broiler chicks, or fish (common carp, *Cyprinus carpio* L. and tilapia, *Tilapia mozambica* P.) (Narayanan 1979). There were no significant differences between the NPV-treated and control organisms in weight gain, food consumption, feed efficiency, weight of different organs, and blood and urine chemistry.

Mass production of NPV

Narayanan (1979) working on the mass production of NPV, found that the optimum dose of inoculum required for obtaining the maximum harvest of virus from fourth-instar larvae was 1.1×10^4 PIB/cup/larva by the diet surface contamination method. The larvae inoculated with this dose yielded the maximum virus of 25×10^9 PIB/larva. There was a

significant positive correlation between the larval weight and the number of polyhedra in NPV-infected larvae. Following the methods described, the NPV of *H. armigera* can be propagated in quantities sufficient for field application. The virus needed to treat 0.4 ha at 250 LE/ha can be obtained from 24 diseased final-instar larvae. Simpler methods of mass production of the virus have been described subsequently by Rabindra and Jayaraj (1985d).

Susceptibility of *H. armigera* to *A. atkinsoni* NPV

Cross-infectivity studies have shown that larvae of *H. armigera* were highly susceptible to a nuclear polyhedrosis virus isolated from *Adisura atkinsoni* Moore. *A. atkinsoni* NPV could produce 100% mortality of *H. armigera* larvae within 4 to 9 days, whereas inoculation of NPV of *H. armigera* in larvae of *A. atkinsoni* resulted in only 40 to 50% mortality in 5 to 11 days. After passage through *H. armigera*, the virus was found to be infective to its original host *A. atkinsoni* (Narayanan, 1985d). The possibility of activation of a latent virus infection in *H. armigera* by a heterologous virus was ruled out by subjecting the larvae to a morphologically distinct heterologous virus isolated from the Indian rice moth *Corcyra cephalonica* Stainton by Rabindra and Subramanian (1973b). Results from preliminary field study have revealed that the NPV of *A. atkinsoni* could produce high mortality in field populations of *H. armigera* (Anon. 1984). These findings indicate the possibility of using the NPV of *A. atkinsoni*, multiplied in *H. armigera*, against both the pests on field bean, on which these insects cause severe loss.

Bacillus thuringiensis

Natural occurrence of *B. thuringiensis* in *H. armigera* (= *H. obsoleta*) was reported as early as 1955 (Majumdar et al. 1955). Preliminary observations on the efficacy of *B. thuringiensis* for the control of *H. armigera* on sunflower revealed only 53.6% mortality (Sundarababu et al. 1970). Certain commercial preparations of *B. thuringiensis* were tested against the pest in laboratory and pot culture experiments. In the laboratory study, Thuricide and Dipel gave 100% mortality, but Bactospeine gave only 20% mortality (Odak et al. 1982). In another study (Dabi et al. 1979), the mortality of third- and fourth-instar larvae from different doses of *B. thuringiensis* was recorded on chickpea. A dose of 12×10^9 and 16×10^9 IU/ha could kill 100% of the third-instar larvae, but the same level of mortality could be achieved in fifth-instar larvae only by a dose of 16×10^9 IU/ha (Table 6).

Field trials

Only a very few trials have been conducted with *B. thuringiensis* for

Table 6. Efficacy of Bacillus thuringiensis *against* H. armigera *on chickpea*

Dose		% mortality at 96 h[1]	
kg/ha	IU/ha	Third instar	Fifth instar
1.00	16 × 10⁹	100.0ᵃ	100.0ᵃ
0.75	12 × 10⁹	100.0ᵃ	90.0ᵇ
0.50	8 × 10⁹	80.0ᵇ	70.0ᶜ
0.25	4 × 10⁹	65.0ᶜ	55.0ᵈ
Control	—	0.0ᵈ	0.0ᵉ

Source: Dabi et al. (1979).

[1]In a column, means followed by the same letters are not different (P = 0.05) by LSD.

Table 7. Efficacy of B. thuringiensis *and insecticides against* H. armigera *on tomato*

Treatment (kg ai/ha)	Mean % fruit infestation[1]
B. thuringiensis	
0.625	9.0ᵇ
1.25	4.5ᵃ
Malathion 1.25	4.6ᵃ
Carbaryl 2.50	0.0ᵃ
Control	18.8ᶜ

Source: Krishnaiah et al. (1981).

[1]In a column, means followed by the same letters are not different (P = 0.05) by LSD.

Heliothis control. On chickpea, Biospray effectively reduced the larval population; however, there was not much increase in the yield (Anon. 1982). Dipel at 0.05% was not effective against the pest on field bean (Krishnaiah et al. 1978). Surulivelu et al. (1978) and Chelliah et al. (1978) also found *B. thuringiensis* to be ineffective in reducing borer damage to field bean and pigeonpea. In tomato, *B. thuringiensis* (Dipel) at 1.25 kg/ha could control the pest to an extent of about 70% (Table 7) but carbaryl at 2.5 kg was found to give significantly better control (Krishnaiah et al. 1981). These results show that there is a need to identify more virulent strains of the bacterium for control of *H. armigera*. Attempts to evolve certain adjuvants or baits might be fruitful.

Other Pathogens

Other pathogens reported from *H. armigera* include *Nosema* sp. (Anon. 1985), *Vairimorpha* sp. (Narayanan 1985b), *Beauveria bassiana* (Balsamo), and *B. brongniartii* (Sacc.) (Jayaramaiah 1981), *Metarhizium anisopliae* (Metschnikoff) (Urs and Govindu 1971), and the mermithid nematode *Ovomermis albicans* (Sieb.) (Bhatnagar et al. 1982). But no serious attempts seem to have been made to field-test these pathogens against *H.*

armigera. Some preliminary information is available on susceptibility of *H. armigera* larvae by growth stage to *Vairimorpha* sp.: larvae of the first four instars were found to be susceptible, while the fifth instar was more or less resistant. In the susceptible larvae, pupal dimension and weight were considerably reduced (Narayanan 1985b).

O. albicans was found to be a common parasite of *Heliothis* larvae collected from weed hosts in grazing areas on Alfisols (Bhatnagar et al. 1982). In one study, 93% of *H. armigera, H. peltigera* Denis and Schiff, and *H. assulta* Guenée larvae collected in August were parasitized by the mermithid. But it did not persist through the season, for few were found after September each year, when *H. armigera* started attacking pulse crops. The mermithid also parasitized *Spodoptera litura* (F.) on groundnut (up to 13%), *S. exigua* on chickpea (up to 59%), *Eucosma critica* M., and *Cydia ptychora* Meyr. on pigeonpea (in low proportions).

DISCUSSION

Efficacy of Pathogens

Of the different pathogens studied, the NPV has been found to be the most promising against *H. armigera.* To maximize the control potential of NPV, the most virulent strain should be selected for mass production and development as a microbial pesticide. The differential virulence of NPV isolates from different geographical locations in India (Pawar et al. 1981) requires detailed investigation. Survey over wide geographical areas covering different cropping and agroecosystems might yield newer strains of *Heliothis* NPV. Inheritable variations in virulence are often found among the strains from diverse geographic locations (Harvey and Volkman 1983), and variants of baculoviruses such as the spruce budworm NPV also arise in laboratory studies when a virus infects an alternative host (Stairs et al. 1981). Variants with enhanced virulence can be identified on the basis of restriction endonuclease analysis of the viral DNA. There is a great need to generate stable variants of the baculovirus that are more effective in the field (Faulkner and Boucias 1985). Mutants of the baculovirus with enhanced virulence can also be generated in tissue culture by growing the wild type virus in the presence of a chemical mutagen. Such studies are needed on the native NPV of *H. armigera* so as to identify the most virulent strain of NPV.

Field Control on Various Crops

NPV

NPV has given encouraging results on chickpea in the field, where *H. armigera* is the only serious pest. There is good scope for increasing the

effectiveness of the virus on different crops by addition of suitable adjuvants, such as brown sugar, chickpea flour, or groundnut oilcake. These materials are cheap and easily available to the Indian farmer.

On other crops like pigeonpea, field bean, and cotton, control of the pest with NPV was not as high as in chickpea, because the fruiting parts on these crops are also attacked by many pests other than *Heliothis*. Better control of these pests can be achieved in several ways. The possibility of using an insecticide-virus bait for tackling the borer complex on pigeonpea and other pulses and the bollworm complex on cotton should be investigated under Indian conditions. Improvements in formulation and application technology can result in better control of the pest. Stability in storage and transport, protective adjuvants, and appropriate timing and methods of application are some of the factors that should be taken into consideration for achieving satisfactory results.

Identification of a virus that can tackle more than one insect species in a pest complex is essential for management of pigeonpea and cotton pests. It is encouraging that we have one such virus—*A. atkinsoni* NPV—which can kill both *H. armigera* and *A. atkinsoni*, the major pod borers of field bean. It may also be possible to tackle the pest complexes by integrating the use of *B. thuringiensis* with NPV (Bell and Romine 1980; Bell 1982).

For the management of *H. armigera* on different crops, attempts to use only the virus can be frustrating. On the contrary, if the use of virus is suitably integrated with other IPM components, such as resistant cultivars, parasites and predators, and chemical toxicants that are compatible with the biocontrol agents, satisfactory and cost-effective control should become a reality. We do have some cultivars in chickpea and pigeonpea which exhibit tolerance to pod borers and other pests, and it would be worthwhile testing these in IPM programs involving the use of microbials. Most of the available information on the relationship of biological control and host-plant resistance deals solely with parasites; very little attention has been given to microbial pathogens (Herzog and Funderburk 1985).

One area that needs immediate attention is development of suitable application technology for dryland crops. More than 60% of the crops on which *H. armigera* occurs are grown under rainfed conditions in India, where water is a constraint to high-volume application of microbial or chemical pesticides. It is necessary to develop a bait formulation that can perform well under ultra-low volume application. Release of virus-infected larvae or virus-contaminated parasitoids can be considered as augmentative methods.

Studies on quantitative host-pathogen relationships as affected by the host plants are vital to the choice of crop for *Heliothis* control with NPV. Such information is available for *Spodoptera litura* (F.) NPV on *hirsutum* and *barbadense* cotton (Santharam 1985). Understanding the various

physical and physiological characteristics of host plants that affect the pathogenicity of the virus to *H. armigera* would help us to develop suitable formulations to reduce, if not prevent, inactivation of the virus on plant surfaces.

B. thuringiensis

Results of field control trials of *B. thuringiensis* have not been very encouraging. There is a need to develop suitable adjuvants for *B. thuringiensis* as well as to identify a more virulent strain with good field persistance.

Although some microsporidians have been identified, there may not be much practical use for them in short-term control, as application of pathogens such as *Vairimorpha necatrix* did not reduce crop damage due to the long incubation period (Fuxa and Brooks 1979; Maddox et al. 1981). However, some impact was realized in subsequent generations from vertical transmission of the pathogen.

In such cases there is a possibility of the pathogen becoming established at the enzootic level. When some limiting host, pathogen, or environmental factor is released to permit the expression, then enzootics develop into epizootics. Since there are many examples of epizootics among arthropod pests, the presumption is that we may somehow manipulate those factors that induce enzootic diseases to become epizootics (Ignoffo 1985).

Acknowledgment

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A Model Genetically Engineered Pesticide: Cloning and Expression of the *Bacillus thuringiensis* subsp. *kurstaki* δ-Endotoxin into *Pseudomonas fluorescens*

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ABSTRACT

The δ-endotoxin gene carried on a *Bam* HI fragment from *Bacillus thuringiensis* (*B.t.*) subsp. *kurstaki* strain HD-1 was cloned into *E. coli* using pBR328. DNA from clones pMAP1 and pMAP2 contained *Bam* HI inserts of 16 kilobases (kb) in opposite orientations. Subcloning of the gene into plasmid vector pUC8 in *E. coli* JM101 led successfully to subclones containing DNA inserts of 8.1 kilobases (kb) (pMAP3) and 4.6kb (pMAP4). Clones pMAP1–pMAP4 retained the pesticidal gene as determined by DNA hybridization, immunological reaction, and pesticidal activity against *Heliothis zea* and *Manduca sexta*. Independently, two isolates of *P. fluorescens*, Ps 3732-37 and 112-12, were isolated from agronomic soil, using strict selection criteria designed to optimize their efficacy as practical "delivery" systems for the *B.t.* gene within the corn rhizosphere. Doubly marked (Rif^r Nal^r) isolates of these *Pseudomonas* strains were field-tested in 1984 and demonstrated excellent translation of laboratory corn root colonization characteristics on several corn varieties. Subcloning of the *B.t.* gene into isolates Ps 3732-3-7 and 112-12 was successful both through introduction on non-self-transmissible plasmids *via* triparental matings and through introduction through a process of chromosomal insertions via homologous recombination using Tn5. These engineered variants of Ps 3732-3-7 and 112-12 express pesticidal levels of the 134,000 molecular weight *B.t.* protein toxin. Field-testing against *Agrotis ipsilon* is planned.

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It is rare for a naturally occurring biological control agent to possess all of the traits required for its practical use in crop systems. Genetic engineering is a potentially excellent tool for enhancing the effectiveness of selective biological control agents. Through the "component" approach that genetic engineering allows, one may be able to combine the best attributes of various naturally occurring organisms to produce a rationally designed biological control agent tailor-made to a specific agronomic application. Conceptually, one could isolate the most effective and highly target-selective pesticidal activities from a "donor" organism and move these active principles into a second organism that possesses more effective and environmentally satisfactory traits as a "delivery" system. If successful, the new organism could retain the desirable traits of both systems while extending practical effectiveness, host range, or both.

This paper describes a model system designed to demonstrate the feasibility of such an approach and describes the rationale for and results of the specific approach taken. The gene from *Bacillus thuringiensis* coding for the δ-endotoxin was chosen as the pesticidal principal due to its well-demonstrated safety as a highly selective commercial agent for the initial control of lepidopteran insect pests. The potential "delivery" systems chosen were selected from indigenous soil organisms using a series of strict criteria to optimize both their effectiveness and safety. The most effective organisms selected, both *Pseudomonas fluorescens* isolates colonizing corn roots, were then transformed with the *B.t.* gene to determine the feasibility of (1) expression of the heterologous gene at effective pesticidal levels and (2) the effectiveness of these engineered organisms as highly targeted pesticides under practical field conditions.

MATERIALS AND METHODS

Criteria for Selection of *Pseudomonas* Root Colonizers

The desirable traits for an effective and environmentally satisfactory biological control agent were used as guidelines to isolate the *Pseudomonas* corn root colonizers. These included a high degree of association specifically with the host root, active colonization of new root growth, resistance to commonly used agricultural chemicals for the corn crop system, resistance to desiccation and other physical factors likely to be encountered in its storage and application, ability to be produced readily in large quantities, and ease of genetic engineering with the available tools of molecular biology.

Other desirable traits are: non-pathogenicity to beneficial organisms, sensitivity to clinical antibiotics and sterilants, limited ability to actively

exchange inserted traits with other organisms, and limited ability to survive independently of the plant root in agronomic soils or limited ability to overwinter in the environment. In addition, the organism should possess genetic markers that allow it to be monitored in the environment. These markers should not include resistance markers for commonly used clinical or agricultural antibiotics.

Using these criteria as guidelines, selection assays were established and agronomic soils were sampled. Early in the investigation of rhizosphere associated soils, it was determined that *Pseudomonas* species were predominant among those that were most likely to match the desired criteria. Two *Pseudomonas fluorescens* isolates, Ps 3732-3-7 and 112-12, were isolated which showed colonization rates as high as 10^7 CFU per fresh weight of corn roots. Through extensive laboratory and greenhouse tests, these isolates were also shown to meet the majority of the above criteria as well (Watrud et al. 1985). Moreover, these isolates lacked indigenous plasmids and lacked the ability to support the conjugative plasmids RP4, N3 and pSa which belong, respectively, to the incompatibility groups IncP, IncN and IncW (Jacob et al. 1977). To date, only derivatives of RSF1010 plasmids have successfully been introduced into Ps 3732-3-7 or 112-12. Such plasmids, which are members of the IncQ group, are not self-transmissible. They require a conjugative plasmid to provide the transfer functions necessary for movement out of the *P. fluorescens* strains.

Cloning of the δ-Endotoxin Gene in *E. coli*

Plasmid DNA of *B. thuringiensis* subsp. *kurstaki* strain HD-1 was isolated, enzymatically restricted with Bam HI, and inserted into the *E. coli* plasmid pBR328. Presumptive transformants were selected for ampicillin resistance and screened with a 21-mer ^{32}P-labeled synthetic nucleotide probe based on N-terminal amino acids 19-25 of the 134,000 molecular weight δ-endotoxin protein (Wong et al. 1983). This protein had been sequenced after isolation from stationary-phase cultures of *B. thuringiensis* subsp. *kurstaki* strain HO-1 and purification in Renograffin gradients and polyacylamide gel electrophoresis (Sharpe et al. 1975). Southern blots (Southern 1975) were used to screen DNA from presumptive transformants. Western blots (Towbin et al. 1979) used to screen protein extracts from putative clones were carried out with a polyclonal antibody prepared against the purified protein. Subcloning fragments of the original clones was accomplished using plasmid vector pUC8 in *E. coli* JM101 (Vieira and Messing 1982). Tests for insect toxicity were performed by diet incorporation against *Manduca sexta* (tobacco hornworm) and *Heliothis zea* (corn earworm).

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Subcloning into *Pseudomonas fluorescens*

Subcloning of the δ-endotoxin gene into *P. fluorescens* was accomplished in several ways, including introduction by means of non-self-transmissible plasmids through triparental matings (Figurski and Helinski 1979) and into the bacterial chromosome by means of suicidal vectors (Selvary and Dyer 1983) and by a process of homologous recombination using the transposon Tn5. Tests for retention of the *B.t.* gene were as above.

Growth Chamber and Field Tests on *Pseudomonas* Isolates

Variants of *Pseudomonas fluorescens* Ps 3732-3-7 and 112-12 were selected which were doubly marked for resistance to rifampicin and naldicic acid. These isolates were applied as inocula to corn seeds and examined for their ability to colonize corn roots in nonsterile soil in the growth chamber and in field plots at St. Charles, Missouri. All studies with engineered Ps 3732-3-7 and 112-12 were done in growth chambers.

RESULTS

DNA from clones pMAP1 and pMAP2 contained *Bam* HI inserts of 16
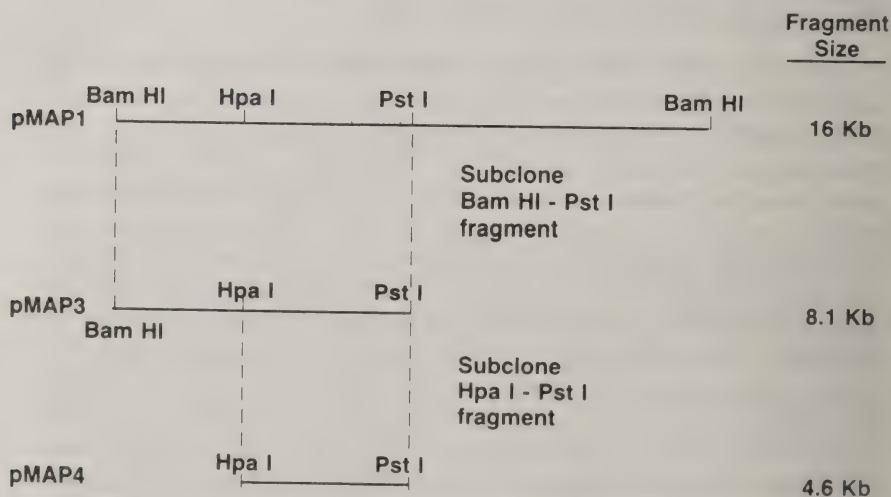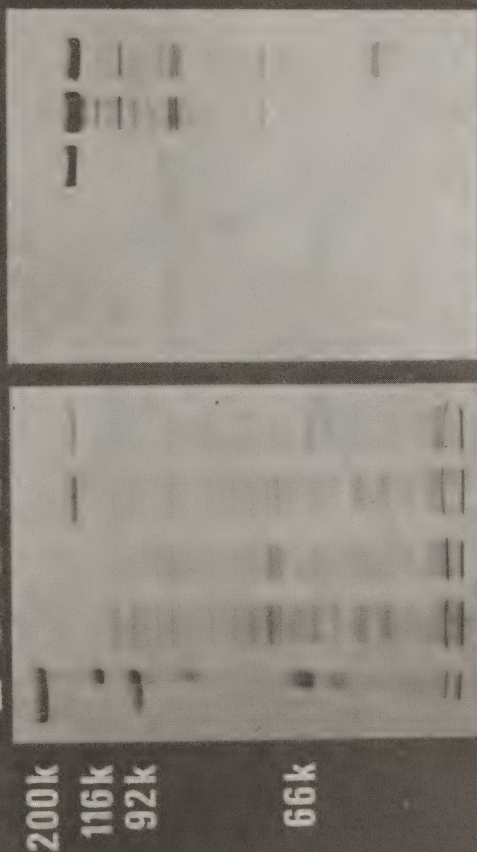
Subcloning of the *B.t.* Toxin Gene

Figure 1. Subcloning of the δ-endotoxin gene from *B. thuringiensis* var. *kurstaki* into pUC8 in *E. coli*. Plasmid vectors pMAP1, pMAP3, and pMAP4, were formed which contained the δ-endotoxin gene on fragments which were, respectively, 16, 8.1 and 4.6 kb in length.

Figure 2. Use of an antibody probe to the δ-endotoxin to demonstrate production of the toxin protein by clones containing pMAP2, pMAP3, or pMAP4. SDS, sodium dodecyl sulfate.
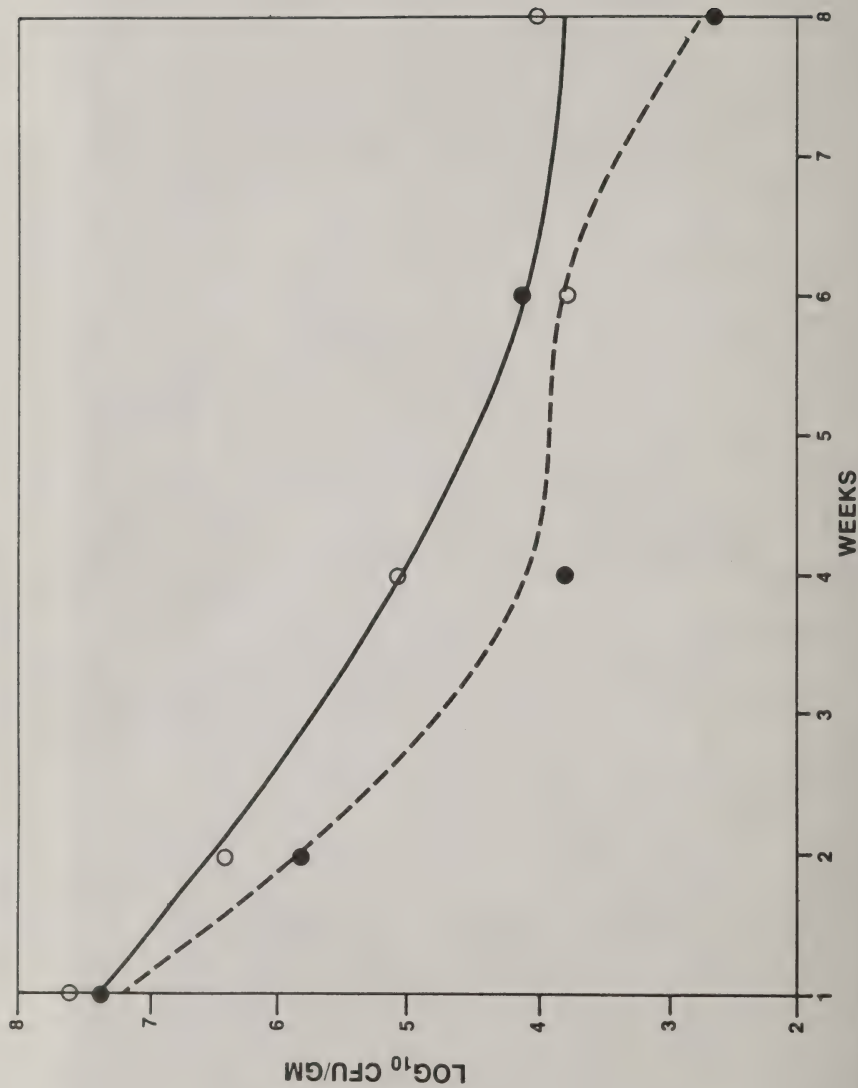
Figure 3. Determination of the survival of parental (○) and engineered (●) derivatives of *P. fluorescens* strain Ps3732-3-7 on the rhizoplane of corn roots grown in nonsterile agronomic soil in growth chambers.
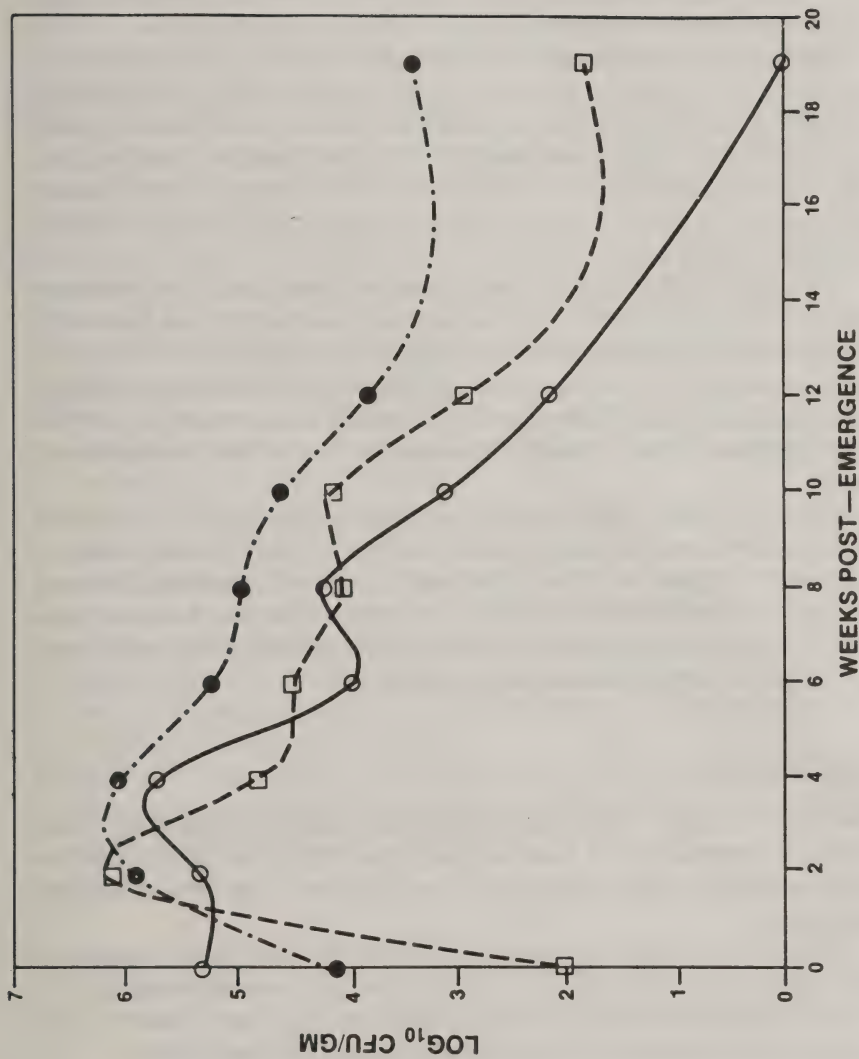
Figure 4. Recovery of a nongenetically engineered Rif^r Nal^r isolate of *P. fluorescens* from the rhizoplane of three cultivars of corn (PN3183, PN3732, and PN3780A) grown in the field at St. Charles, Mo., 1984

kilobases (kb) in opposite orientations which hybridized strongly with the 21-mer nucleotide probe against the N-terminal end of the *B.t.* structural gene. Since this size fragment is obviously much larger than the approximately 3.5 kb needed to encode the toxin protein, subcloning in pUC8 in *E. coli* JM101 was undertaken. Selection of putative transformants in this system was made on the basis of loss of ability to utilize lactose.

Results of subcloning are shown in Figure 1. Utilization of restriction enzymes *Bam* HI and *Pst* I resulted in an 8.1kb fragment, while digestion with *Hpa* I and *Pst* I resulted in a 4.6kb fragment, both of which retained the intact structural gene as shown by DNA hybridization, insect toxicity, and western gel analysis of pMAP3 and pMAP4 respectively. Western gels, shown in Figure 2, demonstrate the expression of the intact 134,000 molecular weight toxin.

Successful subcloning and expression in *Pseudomonas fluorescens* isolates Ps 3732-3-7 and 112-12 was demonstrated in a similar manner.

Survival of parental and engineered derivatives of strain Ps 3732-3-7 on the rhizoplane of corn roots grown in nonsterile agronomic soil in growth chambers is shown in Figure 3, which illustrates that the survival curve of the engineered strain is nearly identical to that of the nonengineered isolate.

Recovery of the double marked nonengineered Ps 3732-3-7 from the rhizoplane of three cultivars of corn in field tests at St. Charles, Missouri, is shown in Figure 4. These data confirm growth chamber data and demonstrate an effective translation of colonization and survival parameters to the field environment. Importantly, the data also demonstrate the decline of the isolates late in the season.

DISCUSSION

The above results, though preliminary, are highly encouraging. Toxic levels of expression of a heterologous gene coding for highly selective insect toxin have been achieved in an effective crop root colonizing organism.

Moreover, the delivery systems, Ps 3732-3-7 and 112-12, appear to demonstrate many of the traits of an effective field colonization microbe. A true test of the effectiveness of this model biocontrol agent, however, will require more extensive tests, particularly in the field crop system.

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Integration of Biological Control into Crop Production Systems

Introduction

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The cropping systems and the associated agricultural practices are often modified with a view to improving the efficiency of crop production systems. The different components of crop production systems, *viz.*, the system of cropping, the crop varieties, agronomic and cultural practices, fertilizers, herbicides and other plant protection chemicals often exert a tremendous influence on both the pests and their natural enemy complex. *Heliothis* spp., being polyphagous, occur on a wide range of host plants like cotton, oilseeds, grain legumes, millets, vegetables, etc. and form part of the herbivore complex in any cropping system. The pest often moves from one crop to another and from weeds to crop plants. For achieving a successful biological control of *Heliothis*, it is a pre-requisite to understand the complex interactions of the pest/natural enemy relationships with the various components of the crop production system.

Any biocontrol technique developed should fit into the existing crop production systems. Conversely, the cropping systems may be altered to reduce the pressure on plants by *Heliothis* and increase the efficiency of natural enemies like parasites, predators and pathogens. Habitat manipulations by changing the cropping systems, crop sequence, intercrops, weed management practices as well as adoption of certain cultural practices may have either a positive or negative influence on the associated herbivore-natural enemy fauna. The effectiveness of the biocontrol strategy may be improved by identifying such manipulations which encourage the establishment of natural enemies and enhance the efficacy of entomopathogens of *Heliothis*.

Host plant resistance— a core tactic in any IPM system— should be compatible with the biocontrol agents. There has been no systematic study to assess the effect of plant resistance on the establishment and success of either native or exotic natural enemies as well as pathogens of *Heliothis*. While plant resistance may help to bring down the *Heliothis* populations to levels easily manageable with biocontrol agents, it may also have adverse effects on the biocontrol agents. Host plant resistance-induced reduction in prey populations may affect the establishment of some paras-

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ites and predators, if the prey diversity falls below the optimum searching capacity of the natural enemy. Host plants may also alter the prey physiology and behavior which may modify the success of natural enemies. Allomonal or toxic resistance factors and morphological defense mechanisms may also limit population of natural enemies that come into physical contact with the host plant.

In most agro-ecosystems herbivores other than *Heliothis* occur and chemical pesticides used against them may destabilize the biological control system. By modifying chemical control practices, we may reduce, if not eliminate, the harmful effects on the biocontrol agents. By suitable choice of a selective pesticide with bio-rational ones which are least ecocidal, selective use of pesticides, timing of treatments, modifying dosages and techniques of formulation and application, we can conserve and improve the efficacy of parasites, predators and pathogens of *Heliothis* spp.

The success of future *Heliothis* biocontrol programs will depend very much on how the above mentioned factors are studied as an integral part of the assessment of the efficacy of a biocontrol agent. In many instances both biocontrol strategies as well as the crop production system might have to be modified or altered to bring about the reduction of *Heliothis* populations below those causing economic injury to the different crop plants.

Habitat Manipulation to Increase Effectiveness of Predators and Parasites

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ABSTRACT

Many crop production practices have either direct or indirect impact on the effectiveness of natural enemies in controlling *Heliothis* spp. This paper deals with both actual and potential habitat manipulations that increase this effectiveness. These management practices can be categorized into three strategic approaches: provision of refugia, provision of alternative foods, and alteration of crop characteristics.

Provision of refugia within the growing season includes "trap cropping," strip treating, interplanting, and other types of polyculture. Refugia for overwintering of natural enemies, at least in temperate climates, are represented by hedgerows, woodlots, and other natural vegetation, as well as crop debris and litter layers resulting from no-till practices. However, care must be taken that such natural enemy refugia do not also serve the same purpose for potential pest species, including pathogens and weed seed.

Provision of alternative foods has also been studied using amino acid rich sprays and/or alternative prey sources for either maintenance or attraction of higher natural enemy densities prior to invasion by *Heliothis*.

Alteration of crop characteristics to enhance natural enemy action against *Heliothis* is another widely used strategy. The tactics involved include cultural practices such as fertilization, planting date, row spacing, and cultivation to indirectly increase beneficial activity by providing refugia, by increasing the growing season prior to invasion by *Heliothis*, and by moderating physical factors (e.g., decreasing temperature, increasing humidity). Selection of varieties has also played a role, where physical or chemical characteristics of the crop have been altered to (1) make *Heliothis* more vulnerable to attack, (2) shift *Heliothis* populations to other crops more favorable to natural enemies, (3) remove plant defense chemicals harmful to beneficials, or (4) provide more suitable refugia or alternative food (e.g., nectar and pollen) to natural enemies of *Heliothis*.

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Examples of the above are presented for natural enemies of *Heliothis* and other similar pest species, together with recommendations for specific research on this topic.

INTRODUCTION

The importance of naturally occurring biological control agents for *Heliothis* spp. is well documented worldwide (Falcon et al. 1968, van den Bosch 1971, Adkisson 1971). In many regions, *Heliothis* spp. are considered insecticide-induced pests, implying that in the absence of pesticides, natural enemies often maintain adequate control of this complex in diverse agricultural systems. Since the topic of pesticide-use impact is discussed elsewhere in this workshop, the focus of our discussion will be on habitat manipulations other than pesticide use. However, it is important to recognize the ever-present interaction of these pesticide-use patterns with such habitat manipulations.

We would like to point out a recent review by Herzog and Funderburk (1985) that contains a large number of references on the subject of habitat manipulation, and that was particularly helpful in preparing this paper.

We can consider four major topics in dealing with habitat manipulation: provision of refugia, provision of alternative foods, provision of chemical stimuli, and alteration of plant characters. Both behavior-modifying chemicals and host-plant resistance compatibility will be discussed in other papers in this section. Thus, this paper will concentrate on the provision of refugia and alternative foods for natural enemies, with some reference to the interaction of these two items with the plant character alterations involved in host-plant resistance.

In much of the research in this area, it is difficult to separate the impact of refugia from that of alternative food supplies (Rabb et al. 1976), particularly when one considers cultural practices that involve cropping systems as opposed to practices involving individual fields.

CULTURAL PRACTICES

Fertilization

Fertilization has been shown to impact the effectiveness of natural enemies. Adkisson (1958) demonstrated significant effects of fertilization on *Heliothis* predators in cotton. Coccinellids, *Orius*, and *Geocoris* all increased with increased fertilizer, while *Nabis* and *Chrysopa* were unaffected. In spite of these increased predator levels, however, *Heliothis* larval densities were higher in the unsprayed, fertilized plots than in sprayed and control plots. Densities of the coccinellids, *Orius* and *Nabis* were not

affected by insecticide sprays, but Adkisson (1958) points out that the experimental plots were surrounded by untreated crops that possibly served as reservoirs for the beneficials. In an interesting study of general predators on cotton, Stone et al. (1984) found that densities of *Geocoris punctipes* (Say) were correlated with square densities and soluble protein concentrations of middle and lower leaves, but not affected by nectar carbohydrate, fatty acid concentrations, or blooms. These results were in agreement with those of Gonzalez et al. (1977) with regard to the importance of squares, but their results were contrary to those of Yokoyama (1978) regarding the importance of extrafloral nectar carbohydrates and fatty acids. This latter discrepancy is attributed to other potential food sources in the experiments by Stone et al. (1984). Similar, although not identical, results were obtained for *Coleomegilla maculata* (DeGeer), *Hippodamia convergens* (Guérin), *Nabis roseipennis* (Reuter), and *Orius insidiosus* (Say). Although fertilizers may increase nutrition to many of the hemipteran predators which also feed on the host plant, increased fertilization may also result in increased foliage. For a number of generalist predators in soybeans, O'Neil (1984) has demonstrated that increased foliage can greatly reduce predator efficiency, since they must search a much greater surface area. Given these opposing functions of fertilization, much more crop- and region-specific research is necessary.

Canopy Enhancement

Canopy development in diverse crops has been shown to impact natural enemies of *Heliothis*. In soybean, as canopy density increases (via effects of seeding rate, row spacing, and planting date), densities of *Geocoris, Nabis,* and spiders increase (Bushman et al. 1984, Sprenkel et al. 1979), and *Heliothis* decrease (Bradley and Van Duyn 1980). In both soybeans and cotton, increased canopy development allowed increased infection by *Nomuraea rileyi* (Farlow) (Burleigh 1975, Sprenkel et al. 1979). At least with cotton, however, reduced canopy density did not affect the *Heliothis* parasite, *Microplitis croceipes* (Cresson) (Burleigh 1975), although soybean genotype did have an impact (Powell and Lampert 1984) on the success of this parasite, as well as infection by *Bacillus thuringiensis* (Berliner) (Bell 1978).

Plant Host Characteristics

It should be noted that both chemical and physical attributes of host plants play a major, yet poorly studied, role in natural enemy efficiency. The negative impact of plant defensive chemicals, such as α-tomatine in tomato, on the *Heliothis* parasite, *Hyposoter exiguae* Vier is well documented (Campbell and Duffy 1979). Morphological characters, such as

trichome density, affect both predation (*Chrysopa rufilabris* (Burmeister), Treacy et al. 1983) and parasitism (*Trichogramma* spp., Rabb and Bradley 1968, Elsey and Chaplin 1978, Treacy et al. 1983). In a study of several major crops, Keller (1985) has demonstrated that these trichomes directly impede searching rates by *Trichogramma* in proportion to their densities and patterns.

ALTERNATIVE FOODS

The provision of alternative food for natural enemies has been accomplished through direct application. Sprays of nutrient solution have increased *Chrysopa carnea* (Stephens) populations (see review by Hagen et al. 1970, Hagen and Hale 1974). Hagen and Hale (1974) note that sugar sprays alone can be used to attract and maintain both coccinellids and *Chrysopa* adults, but that complex sprays of sugar and Wheast® also induce oogenesis and oviposition, providing the beneficial larvae necessary to reduce *Heliothis* in cotton. Hopefully, research on artificial diets and nutrition of entomophagous insects, such as that by Hoffman et al. (1975) for *Trichogramma*, and Yazgan (1972) for *Itoplectis conquisitor* (Say) will be continued and expanded (see reviews by Rabb et al. 1976, House 1977, Stinner 1977), particularly in conjunction with inoculative or inundative releases of target and nontarget prey to maintain parasite levels during periods of low prey availability. Considering the success of this approach with *Trichogramma* and *Pieris* (Parker and Pinnell 1972), it is surprising that this tactic has not been more fully explored.

POLYCULTURE

Within individual fields, both trap cropping and interplanting have been shown to increase the effectiveness of natural enemies of *Heliothis*, both directly and indirectly. Early-planted trap crops or small plots of more preferred host plants can attract and concentrate overwintered *Heliothis* populations in small areas where they can be treated with conventional pesticides, thereby preserving the natural enemies in the remainder of the field (Newsom 1975, Newsom and Herzog 1977).

With the increased interest in both "landscape ecology" and polyculture, numerous studies have been conducted on the impact of strip-cutting, strip-cropping, intercropping, and weed management on natural enemies of *Heliothis*. Over 20 years ago, Stern and colleagues (Stern et al. 1964, van den Bosch and Stern 1969) demonstrated that strip-cropping of alfalfa in California greatly increased populations of nabids, chrysopids, anthocorids, and coccinellids. Stern (1969) further showed that if alfalfa were

strip-cropped and interplanted with cotton, the benefits of these increased natural enemies could be transferred to the cotton.

In similar studies in Oklahoma with a sorghum-cotton intercropping, Robinson et al. (1972a, b) found increased predator populations and cotton yield. On average, there were from 1.2 to 1.5 times as many coccinellids, *Chrysopa*, nabids, and spiders in cotton adjacent to sorghum than in cotton grown alone. Surprisingly, cotton grown with corn, soybean, alfalfa, or peanut averaged slightly fewer predators than cotton alone. Cotton yields were generally in agreement with predator densities. Highest yields were observed in the sorghum/cotton system. Yields lower than cotton alone were observed for the cotton planted adjacent to corn, soybean, alfalfa, and peanut. This reinforces the concept voiced by Southwood (1972) that it is not diversity itself that is important, but the specific kinds of diversity present. Reviews by Laster (1974) and King et al. (1982) provide additional credence to this approach, particularly in regions of the world where intercropping and polyculture are more usual and accepted than in the USA.

WEED MANAGEMENT

The impact of weed management for natural enemy manipulation has also been considered, both in theory and practice. Given the relatively new attention to minimum and no-till systems (and the resultant increase in herbicide use), such studies are sorely needed. King et al. (1982) reported unpublished data of E.A. Stadelbacher in Mississippi demonstrating that the numbers of beneficials found in old soybean and cotton fields were proportional to the stand density of winter and spring annuals. The general subject of weed management and natural enemies has been addressed in reviews by Altieri and colleagues (Altieri et al. 1977, Altieri and Whitcomb 1979). Direct relationships between natural enemies and weeds have been reported for soybeans in Indiana (Shelton and Edwards 1983), where fields with a mixture of grass and broadleaf weeds had approximately double the number of beneficials as weed-free fields. These natural enemies included *Coleomegilla, Orius, Nabis,* and carabids of the genus *Harpalus,* all known predators of *Heliothis.*

RECOMMENDATIONS

Although work is sorely needed in all areas of habitat-management effects on natural enemies of *Heliothis,* several general topics would seem to be paramount.

First would be a considerable increase in efforts to understand the relationships between natural enemies (and their efficacy) and the host

plants that provide them a place to live, and often some nutrition as well. Such studies are of foremost importance, because the results could be of immediate use in designing management systems for enhancement of these natural enemies.

Second, we need much additional knowledge on natural enemy nutrition, not only for mass-rearing programs, but also to develop the potential for food supplement technology, to avoid the documented flight (or death) of many of these beneficial species during periods of low *Heliothis* densities. This is particularly important for managing a species as mobile and polyphagous as *Heliothis*.

Finally, we need new, intensive research on overwintering. With few exceptions, there is almost no knowledge of this process for natural enemies. For example, in recent studies with naturally occurring *Trichogramma exiguum* Pinto and Platner in North Carolina, Keller (1985) observed emergence in the field during all months of the year, including midwinter. In addition, he measured successful development times in excess of 4 months on a range of noctuid hosts, and adult longevity averaging almost 1 month during February and March, leading him to conclude that this parasite overwinters via prolonged development and adult longevity. Although it appears ubiquitous in this region, where are its physical refugia and its major hosts during this period? These same basic questions could be asked for almost all natural enemies of *Heliothis* in temperate climates.

In conclusion, habitat manipulation as a strategy for managing *Heliothis* with natural enemies is widely used. Due to the mobile and polyphagous nature of this pest complex, this strategy offers real potential, but much more can be done when we more fully understand the impacts and interactions provoked by different habitat manipulations.

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Compatibility of Host-Plant Resistance and Biological Control of *Heliothis* spp. (Lep.: Noctuidae)[a]

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ABSTRACT

The available literature concerning the compatibility of host-plant resistance and biological control, with particular reference to *Heliothis* spp., is reviewed. There has been a large amount of successful research on host-plant resistance and biological control as individual components for the management of *Heliothis* spp., and it has often been postulated that these components are compatible, or even synergistic. However, there are few reports of experimentation to test their compatibility. Research done at ICRISAT on the effects of host-plant resistance on parasitism in *Heliothis armigera* Hübner larvae on pigeonpea and chickpea is reviewed. It is suggested that the effect of host-plant resistance on the biocontrol elements must be tested in large plot field trials before these components are used in integrated pest management projects.

The widely publicized disasters in which *Heliothis* spp. developed resistance to insecticides in the Americas (Adkisson 1971) and in Australia (Wilson 1974) stimulated research on the alternatives to insecticides for the management of these and other pests. Biological control (biocontrol) and host-plant resistance (HPR) are both very attractive components of integrated pest management (IPM) which have received substantially increased research attention in recent years. This paper reviews the research into the effect of HPR on biocontrol and their compatibility or otherwise in the control of *Heliothis* spp. Throughout this paper, biocontrol is used in its wider sense, to include the endemic control elements as well as actively introduced parasites, predators, and insect pathogens.

THEORETICAL CONSIDERATIONS

Many entomologists have theorized on the influence of HPR on biocontrol; one of the earliest, and perhaps the most pragmatic, was Painter (1951), who wrote:

> There appear to be only a few cases on record in which a study has been made of the influence of plant host on insect parasites or predators by way of the insect host . . . The information available indicates that the relationship between resistant varieties of plants and the insect parasites of the pests affected by the plant resistance may take two or more trends. First, reduction of the population level of the insect hosts might make it difficult for the parasites to find them and thus would have an adverse effect on biological control by parasites. Second, the profound effect on the physiology of the host which may result from feeding on resistant plants, might affect the establishment of insect parasites favourably, or unfavourably. Again the effect of resistant plants on host size would influence the prolificacy, size and perhaps sex of the insect parasite. Thus any relationship between resistant plant varieties and insect parasites cannot be predicted with certainty before hand but will need to be worked out in each individual case.

Although Painter stressed that the effects of HPR on biocontrol may be adverse in some cases, subsequent reviewers have tended to be optimistic, concentrating upon theories that stress the compatibility of the components. For example, Adkisson and Dyck (1980), when reviewing the role of resistant cultivars in pest management systems, considered that "resistant varieties are highly compatible with biological control." They postulated that the integration of HPR and biocontrol into a pest management system may result in synergism. The reduced rate of pest increase on a resistant cultivar may greatly prolong the time required for the pest's population to reach the economic, or action, threshold for insecticide use. Such delay offers an increased opportunity for the biocontrol elements to become established and effective. In some cases such combined effects of HPR and biocontrol may obviate the need for insecticide use.

A similar synergistic effect may also occur when the antibiosis of a resistant plant prolongs the nymphal period of a pest, or weakens it, so increasing its vulnerability to biocontrol elements, including the insect pathogens (Maxwell 1972). Morphological characters associated with host resistance may also provide a favorable environment for increased predation and parasitism, as in the open-headed, partially resistant sorghum hybrids (Teetes 1976).

PUBLISHED REPORTS

There are many published reports on the occurrence, development and utility of host plant resistance against *Heliothis* spp. in a range of crops.

These reports have been reviewed and summarized by Rogers (1982) and by Lukefahr (1982), who was not optimistic about the short-term utility of HPR for *Heliothis* spp. management:

> *Heliothis* spp. have a wide host range and are multigeneration pests. Therefore a population may build up on one crop and then move to another in large numbers. Since the population increase may not occur within the crop as in monophagous pests, high levels of resistance are required if populations are to be stabilized below the economic threshold level . . . . Progress in host-plant resistance research is a long-term proposition and requires considerable resources. With the limited financial resources available today, many host-plant resistance projects have suffered. Unfortunately, funding is available only when a crisis is looming and with the availability of the synthetic pyrethroids, there is no crisis on the horizon . . . . However, there are many crops where pesticide is not part of the production system. These are usually crops that have a low cash value per unit of land or crops grown in regions where growers do not have access to chemicals or the equipment to apply them. It is in these situations that host-plant resistance will have its potential impact.

There are also many published reports concerned with the biocontrol agents that attack *Heliothis* spp. King et al. (1982), provided a comprehensive summary of the literature and the prospects for utilization of parasites and predators in the management of *Heliothis* spp. Similarly, McKinley (1982) and Bell (1982) reviewed the prospects for the use of pathogens in the management of these pests.

However, there appear to be few publications that report the results of studies on the effects of HPR on biocontrol against *Heliothis* spp. Wiseman (1982), when reviewing the use of crop cultivars that are resistant to *Heliothis* spp. in pest management systems, reported, "Interactions that involve *Heliothis* resistant plant and predators or parasites have not been published." Consequently he was forced to utilize the frequently quoted reference of Starks et al. (1972), which involved studies of an aphid and its parasite on resistant and susceptible barley!

At the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), a computer search of the available literature, as abstracted in the *Review of Applied Entomology* from 1972 to July 1985 (84,976 references), revealed an abundance of references reporting work on *Heliothis* spp. (3,321), but of these only 6 referred to both HPR and biocontrol. Of these six publications, two were general reports referring to HPR and biocontrol agents separately, with no consideration of their interaction. Two more referred to work carried out at ICRISAT; this work will be reviewed in the next section. The remaining two reports follow.

Mussett et al. (1979) studied the populations of predatory arthropods on a standard commercial variety of cotton and on experimental varieties that had been bred for resistance to *Heliothis* spp. in Oklahoma fields. They found a 68% reduction of predatory arthropods on the resistant cotton when compared with the populations on the standard variety. They

were not able to determine whether this predator reduction was caused by a reduction in prey availability (*Psallus seriatus* [Reut] populations, which formed part of the prey, were also reduced on the resistant cotton) or by some antibiotic factors in the resistant cottons.

The second report was by Lingren et al. (1978), who studied augmentative releases of the *Heliothis virescens* (F.) larval parasite, *Campoletis sonorensis* (Cameron), on cotton lines that were resistant and susceptible to *H. virescens* in field cages in Texas. Here HPR and biocontrol were found to be compatible, for parasitism was heavy and F_2 larval populations failed to develop on the resistant cotton.

There are also a few reports concerning investigations on the mechanisms/chemicals in host plants that influence searching behavior by the parasites of *Heliothis* spp.—for instance, those by Elzen et al. (1984a, 1984b)—which may help us to understand some plant × biocontrol interactions. Such studies also appear to be few and far between.

STUDIES AT ICRISAT

Heliothis armigera Hübner is a pest on all five of ICRISAT's mandate crops—pigeonpea, chickpea, sorghum, millet, and groundnuts, but damage is most severe on the first two of these. It has been estimated that the cost of losses of pigeonpea and chickpea to *H. armigera* in India may exceed $300 million per year (Reed and Pawar 1982). The heavy damage caused by *H. armigera* on these crops may be partially a result of the relatively low parasitoid activity. More than 26% of the eggs of *H. armigera* were found to be parasitized by *Trichogramma* spp. on sorghum but only 0.1% on pigeonpea and none on chickpea. Parasitism in *H. armigera* larvae was found to average 27% on sorghum but only 11% on pigeonpea (Bhatnagar et al. 1982). Although at least 26 parasitoids and many predators have been recorded from *H. armigera* in central India, there are massive outbreaks of this pest on pigeonpea. Such outbreaks are not the result of the disruption of natural enemies by insecticide use, for few farmers use pesticide on these crops.

Research at ICRISAT has been primarily directed towards identifying and developing pigeonpea and chickpea genotypes that have resistance or tolerance to attacks by *H. armigera* and other pests. Both of these crops are typical of Lukefahr's (1982) concept of crops on which HPR is likely to have a "potential impact." This research has been particularly successful in chickpea, for several lines with considerable resistance have been selected and developed (Lateef 1985). There is also a considerable range of susceptibility/resistance in pigeonpea, but problems of outcrossing have limited progress in breeding for resistance in this crop (Bhatnagar et al. 1982).

Preliminary field studies at ICRISAT in which *H. armigera* larvae were

collected from resistant and susceptible genotypes tended to indicate lower parasitism rates from the resistant genotypes both on chickpea (Sithanantham et al. 1982) and on pigeonpea (Sithanantham et al. 1983). Data from these and subsequent studies have shown that the percentage parasitism rates in larvae collected from the resistant genotypes were lower than in those collected from the susceptible genotypes in almost all samples. These differences were significant for all larvae collected from pigeonpea, but only for older larvae collected from chickpea. However, the reductions in populations of larvae caused by plant resistance were great enough to more than offset the small reductions in mortality due to parasitism. All of these data were collected from small plot (< 20 m) trials, so interplot effects may have been important.

The mobility of *Heliothis* spp. and their natural enemies may cause substantial, and misleading, interplot effects where small plots are used. To determine the real effects of plant resistance on biocontrol, it will be necessary to record data from large (ca. 0.5 ha) plots of resistant and susceptible genotypes. The differences in parasitism/predation on such plots may simply reflect the differences in the density of the *H. armigera* populations, for the resistant genotypes will have lower populations of the pest. To determine whether the differences are other than density-dependent effects, it will be necessary to inoculate with eggs or larvae to ensure that approximately equal populations of the pest are available on both resistant and susceptible genotypes. We hope to collect such data at ICRISAT in the future.

CONCLUSIONS

In common with several other aspects of IPM, the effect of HPR on biocontrol is frequently discussed but seldom subjected to research in the fields. There is a large quantity of published data on HPR and on biocontrol of *Heliothis* spp. from several crops, but almost all report HPR and biocontrol as separate components. Specialization has ensured that HPR and biocontrol research is usually handled by workers in separate departments or institutions. If IPM is to become a reality, the various components must be evaluated in combination to determine whether they are compatible. Such testing can be initiated in cages or on small plots on research stations, but eventually we must obtain data from large fields replicated under typical farming conditions.

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Modifying Chemical Control Practices to Preserve Natural Enemies

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ABSTRACT

Insects differ in their metabolic capabilities in relation to their diets. Oxidative processes are important in plant feeders, while carnivores rely more on hydrolytic mechanisms. Certain insecticide types are metabolized primarily through oxidative routes, while others are metabolized hydrolytically. This presentation examines the concept that hydrolytically metabolized insecticides are safer for beneficial insects and are therefore more appropriate for use in integrated pest management systems which stress conservation of natural enemies or include release of beneficial organisms.

It is known that insecticidal controls aimed at a particular species can have unwanted effects. These include destruction of natural enemies resulting in resurgence of the pest following chemical control, release of secondary pests, development of resistance in pest populations, adverse environmental effects, etc. (Metcalf 1980). In most cases, the broad spectrum insecticides used in modern agriculture are more toxic to entomophages than to pests. At the same time it is well to remember that there are situations where the use of insecticides is the only means available to achieve economical production of a crop. This occurs for a variety of reasons, among which is our inability to obtain the same goal via biological means. The challenge is to maximize the benefits associated with the use of both biological and chemical controls while minimizing the negative impacts of the latter.

In this paper we discuss this problem from the standpoint of attempting to relate physiological differences among pest and beneficial species to their interaction with insecticides. Since all insect species are not equally susceptible to all insecticides, a general understanding of how a pest and its

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natural enemies respond to different types of insecticides may facilitate design of selective control methods.

Insects possess several defense mechanisms that enable them to cope with dietary adversities they face, such as natural toxic substances. By exploiting differences in these mechanisms among species it may be possible to identify and/or develop insecticides minimally toxic to beneficial insects, so as to tilt the selectivity equation to the disadvantage of pests. If this can be achieved, a certain level of chemical control of insect pests may be compatible with biological control programs which utilize beneficial insects.

In Texas, the cotton insect pest complex presents a major problem to economical production. Early season control of the boll weevil, *Anthonomus grandis* Boheman, an immigrant pest for which nonchemical control measures have only limited potential for management, results in reduction or elimination of the beneficial insect complex that usually maintain *Heliothis* spp. populations at tolerable levels. When insecticide treatments for the boll weevils are initiated, growers find themselves having to apply insecticides for *Heliothis* as well. Thus, our goal is to find chemicals useful against *Heliothis* while sparing the natural enemies that normally are important components of *Heliothis* management programs. If this can be done, it is possible that *Heliothis* populations can be managed with less dependence on chemical insecticides.

Our approach to the problem is based on some ideas concerning the biochemistry of insect : host plant relationships and accumulated knowledge concerning insect : insecticide interactions. The central point is that insects utilizing different food sources have different metabolic requirements. Plant eaters have to defend themselves against natural toxins in their host plants. Conversely, carnivores such as predators and parasites must contend with diets that are high in protein and fat and therefore very different from those of phytophagous insects. It is well known that insects metabolize insecticides by the same enzymatic processes they use for the natural toxins in their diets. Plant feeders rely heavily on the use of mixed function oxidases (MFOs) to degrade both plant allelochemicals and insecticides. On the other hand, carnivores metabolize insecticides and other components of their diet largely by hydrolytic processes, reactions catalyzed by esterases and related hydrolytic enzymes.

The solution then becomes obvious. Ideal insecticides would be those detoxified by the metabolic processes best developed in parasites and predators and not by the processes most efficient in the pests. Unfortunately, selectivity based on these principles has not been an important consideration in insecticide development. Instead, insecticides efficacious against pest species have been developed with almost no consideration of their possible adverse effects on natural enemies.

The critical experiments on insecticide selectivity were reported by Krieger et al. (1971). In this work the relative activities of oxidative detoxifying enzymes (mixed function oxidases or MFOs) were measured in larvae of a variety of lepidopterous insects and correlated with degree of feeding specificity. They found that among the species evaluated there is a direct relationship between range of plant host fed upon and MFO activity. Narrow-spectrum feeders have limited MFO activity; broad-spectrum feeders have more enzyme or more efficient enzyme—certainly more effective MFOs.

These ideas were further developed in a study by Brattsten et al. (1977). The authors showed that the MFO enzymes of *Spodoptera eridania*, a polyphagous insect, were induced to higher levels by numerous plant allelochemicals. They also showed that induction increased tolerance to nicotine, a plant allelochemical sometimes used as an insecticide. Thus, the same enzymes provide a defense to both allelochemicals and insecticides.

The variation in feeding habit between multihost and single host insects parallels variation in response to oxidatively metabolized insecticides. For example, insects such as the boll weevil or the codling moth which feed on hosts within a single plant family are usually quite sensitive to oxidatively metabolized insecticides. In contrast, polyphagous feeders such as *Heliothis* and *Spodoptera* are often more tolerant to such insecticides.

Not only are there differences in detoxification capabilities among species, there are differences relating to life stage within a species. For example, methyl parathion is very toxic to first instar *Heliothis* larvae and adults, but almost nontoxic to the voracious fifth instar (mature) larvae. A rationale that might explain these findings is that only the stage which feeds heavily on plant materials, the mature larva, is a good metabolizer.

In contrast, the pyrethroid insecticide permethrin, an insecticide quite refractory to oxidative metabolism, is nearly equal in toxicity to all life stages of *Heliothis*. In terms of controlling a pest species with a strong capacity for oxidative metabolism, permethrin might have the advantage of not losing efficacy for the most damaging stage.

What we have done in our work is to extend the Krieger model for monophagous and polyphagous insects to include nonphytophagous insects. If monophagous insects are generally less efficient oxidizers than polyphagous insects, then carnivores and nectar or pollen feeders should be even more inefficient oxidizers. A diminished capacity for oxidative detoxifying activity may explain the great sensitivity of nonphytophagous insects to most insecticides.

Based on this hypothesis we have constructed a model describing the hypothetical relative levels of MFOs and esterases in pest, predator and parasite species (Table 1). The term esterase refers to the entire group of enzymes which hydrolyze such substances as fatty acid esters and bonds

Table 1. Hypothetical metabolic capabilities of several insect types

Type	Oxidase	Esterase
Plant feeder	High	Moderate
Predator	Low	Moderate-high
Parasite	Very low	Moderate
Pollinator	Nil	Moderate-low

between amino acids. These should be present in all insects, particularly carnivores. On this basis, predators and parasites should have better esterases than plant feeders. The diets of pollinators and other adult insects with similar feeding habits are largely restricted to carbohydrates. Such insects should be poor detoxifiers and the long record of high sensitivity of these insects to easily metabolized insecticides confirms this hypothesis.

If we relate the capabilities of insects to detoxify insecticides to their feeding habits, a clear pattern emerges. Oxidatively metabolized insecticides will kill beneficials better than they kill pests because beneficials are poorer oxidizers. Conversely, hydrolytically metabolized insecticides are similarly toxic to pests and beneficials. Finally, nonmetabolized insecticides such as cyclodienes ought to be similar in toxicity to all insects—pollinators as well as pests, parasites, and predators. For example, when chlorinated insecticides were widely used on forage crops there were no particularly selective effects against beneficials and pollinators. However, when the organochlorines were replaced with the easily metabolized organophosphates and carbamates because of residue problems with the former, the pollinators were decimated and it became necessary to devise whole new management schemes for these crops.

The next point to consider is the pathway, oxidation or hydrolysis, by which insecticides are metabolized. A brief generalized summary of metabolic pathway by insecticide type is shown in Table 2. Several insecticide types, most importantly the widely used phosphorothionates and aryl carbamates, are detoxified oxidatively. Other types such as phosphates and oxime carbamates are more susceptible to hydrolytic metabolism. The synthetic pyrethroids are metabolized hydrolytically or not at all and

Table 2. Hypothetical major route of insecticide metabolism by type

Insecticide type	Metabolism
Phosphorothionate (P = S)	Oxidative
Phosphate (P=O)	Hydrolytic
Aryl carbamate	Oxidative
Oxime carbamate	Hydrolytic
Synthetic pyrethroid	Hydrolytic

among available insecticides may have the greatest promise for inclusion in IPM programs.

The insects we used to test the above hypotheses are as follows: our pest was the tobacco budworm, *Heliothis virescens* (F.), tested as third instar larvae, the predator was *Chrysopa carnea* (Stephens), tested as second instar larvae, and the parasite was *Campoletis sonorensis* (Carlson), tested as adult males (Plapp and Vinson 1977 and Plapp and Bull 1978).

Table 3. *Toxicity and selectivity of a number of insecticides tested with* H. virescens, C. carnea *and* C. campoletis

TYPE and Insecticide	LC50s (μ g insecticide/vial)			Pest Predator	Pest Parasite
	Pest	Predator	Parasite		
PHOSPHOROTHIONATES					
Methyl parathion	28	0.26	0.04	108	700
Ethyl parathion	78	0.48	0.08	163	975
EPN	263	1.66	0.13	142	1815
PHOSPHATES					
Profenofos	6	0.78	0.51	8	12
Acephate	36	5.6	3.5	6	10
CARBAMATES					
Carbaryl (Aryl)	889	104	1.48	9	600
Methomyl (Oxime)	2.3	2.7	0.98	0.9	2
PYRETHROIDS					
Permethrin	5.7	10	0.31	0.6	19
Fenvalerate	2.7	73	1.76	0.04	1.7
Cypermethrin	2.7	22	0.48	0.12	5

[1]Adapted from Plapp and Vinson (1977) and Plapp and Bull (1978).

Insects were exposed to films of insecticide in glass vials to determine the relative toxicity of each insecticide to each insect. The results (Table 3) indicated that the three oxidatively metabolized phosphorothionates (P=S) were much more toxic to the predator and the parasite than to the pest. For example, the LC_{50} of methyl parathion for the pest (28 μ g/vial) is 108 times more than that for *Chrysopa* and 700 times more than that for the parasite. For ethyl parathion, the toxicity ratios are 163 and 975 for the predator and for the parasite; for EPN the values are 142 and 1,815. Clearly, the use of these insecticides to kill a pest would inflict heavy damage on populations of beneficials.

Two phosphates (P=O) were tested. These insecticides were only 6–12 times as toxic to the predator and the parasite as to the pest. In other words, these insecticides show much less selectivity against the beneficials than did the phosphorothionates.

The aryl carbamate, carbaryl, is very low in toxicity to the pest (LC_{50} of

889 μg/vial), but highly toxic to the parasite (LC$_{50}$ of 1.48 μg/vial). Methomyl, an oxime carbamate metabolized both oxidatively and hydrolytically, is nearly equal in toxicity to all three test insects. Clearly, methomyl represents an improvement over carbaryl in terms of pest : beneficial selectivity.

The synthetic pyrethroids tested are all highly toxic to the pest with LC$_{50}$s ranging from 2.7 to 5.7 micrograms per vial and have similar toxicity to the parasite (0.31–1.76 micrograms per vial).

However, for *C. carnea* the LC$_{50}$s ranged from 10 to 73 micrograms per vial. This means these insecticides are more toxic to the pest than to the predator. As far as *C. carnea* is concerned, we now have truly selective insecticides, ones that will kill the pest but spare the predator. The safest pyrethroid, fenvalerate, is 25 times as toxic to the pest as to the predator.

Biochemical data with *C. carnea* that support these results have been reported. Ishaaya and Casida (1981) described pyrethroid esterases in this insect which may contribute to its high tolerance to pyrethroids.

Additional data confirming the enzymatic basis for pest : predator selectivity were reported by Mullin et al. (1982). In their study they compared detoxifying enzyme activities in susceptible and resistant populations of a pest spider mite, *Tetranychus urticae*, and a resistant predator mite, *Amblyseius fallacis*. Table 4 shows activity for detoxifying enzymes in the pest and predator mites. Activity is presented on the basis of 100% of that in the susceptible pest. These data show much higher MFO activity in the plant feeding pest than in the predator and similar esterase levels in susceptible strains of both species. However, there is a 7-fold increase in esterase activity in the resistant predator. Obviously, insecticides metabolized hydrolytically might be safe for this animal. These data are important in that they clearly show a basis for insecticide selectivity. As we found with bioassays, Mullin and coworkers showed biochemically that certain pests are better oxidizers than predators, while both are similar in hydrolyzing enzymes. These authors further showed that the resistant predator is a better detoxifier than the susceptible predator and thus, could be very useful in IPM programs.

Table 4. *Relative levels of detoxification enzymes in pest and predator mites*[1]

Species	Oxidase		Esterase	
	Susceptible	Resistant	Susceptible	Resistant
Pest	100	120	100	80
Predator	19	16	80	560

[1]Adapted from Mullin et al. (1982).

Several other recent studies have provided evidence for greater safety of certain insecticides, most notably the pyrethroids, for beneficial insects. During the past few years, adults of the braconid larval parasitoid *Microplitis croceipes* (Cresson) have been commonly observed in treated cotton fields in Mississippi and Arkansas where pyrethroids are used as the predominant means of insecticidal control of *Heliothis*. Examinations of samples of parasitized *Heliothis* larvae collected from these areas revealed that this species was by far the most prevalent of parasitic species identified.

Subsequent controlled studies in the field by Powell and Scott (1985), using adult *Microplitis* caged for 24 h on cotton plants which were newly treated at recommended rates of insecticides, demonstrated that this insect was unusually tolerant of two synthetic pyrethroids (flucythrinate and fenvalerate) and a carbamate (thiodicarb) that are all effective *Heliothis* larvicides.

More recently, Powell et al. (1986) conducted studies to determine the spectrum of susceptibility of *Microplitis* adults to different kinds of pesticides used to protect cotton from various pests (Table 5). The results demonstrated that organophosphorus (OP) compounds, especially those metabolized primarily through oxidative routes, were generally the most toxic of the insecticides tested. Dicrotophos (a phosphate) and methomyl (an oxime carbamate), which are detoxified mostly via hydrolytic process, were about equal in toxicity to the pyrethroids. The pyrethroids tested all demonstrated more favorable selective toxicity properties than those of

Table 5. Toxicity of different insecticides to Microplitis croceipes *adults*[1]

Insecticide	24 hr LD50 (μg/insect)	Relative toxicity, %
Methyl/ethyl parathion	0.013	100
Chlorpyrifos	0.022	59.1
Azinphosmethyl	0.026	50.0
Malathion	0.052	25.0
Dimethoate	0.069	21.7
Sulprofos	0.137	9.5
Permethrin	0.203	6.4
Toxaphene	0.246	5.3
Dicrotophos	0.309	4.2
Flucythrinate	0.397	3.3
Methomyl	0.405	3.2
Fenvalerate	0.940	1.4
Chlordimeform	2.5	0.5
Diflubenzuron	2.5	0.5
Thiodicarb	2.5	0.5

[1]Data adapted from Powell et al. (1986) and D.L. Bull, unpublished studies.

most OP insecticides. Chlordimeform, diflubenzuron, and thiodicarb were essentially inactive. The inactivity of chlordimeform and diflubenzuron was not unexpected, because these compounds have specialized modes of action with little contact toxicity. However, the low level of toxicity of thiodicarb is very interesting since this insecticide has excellent activity against *Heliothis* larvae. Thiodicarb is a carbamate that most likely is detoxified by hydrolytic processes.

There is considerable interest in the use of inundative aerial releases of the egg parasite *Trichogramma* to control *Heliothis* spp. on crops. Unfortunately, these parasites are highly susceptible to many insecticides and all attempts to evaluate releases of *Trichogramma pretiosum* in cotton fields contaminated with insecticides have either failed or met with limited success. In an effort to better understand problems encountered in field releases, Bull and House (1983) and Bull and Coleman (1985) conducted studies in the laboratory and greenhouse to evaluate the performance of this parasite following exposure to some insecticides used to control cotton pests.

Insecticides used in these tests were standard commercial formulations of methomyl, chlordimeform, permethrin, thiodicarb, and methyl parathion. Preliminary laboratory tests of the effects of these insecticides on the hatch of tobacco budworm eggs used as host for *Trichogramma* demonstrated that methomyl, thiodicarb, and chlordimeform had good ovicidal activity throughout the range of doses evaluated. Permethrin was active at the 0.2 kg/ha dose level, and methyl parathion was essentially inactive even at the highest treatment level. Tests on the effects of the same insecticides on the parasitism of treated host eggs indicated that when compared with the control, methomyl, permethrin and methyl parathion at all treatment levels severely reduced parasitism of eggs that were treated *before* exposure to parasites. There was somewhat less reduction of parasitism by chlordimeform, and thiodicarb did not affect parasitism at any of the doses tested. However, when eggs were treated *after* they had been exposed to the parasites, there were no apparent effects on the development of immature stages of the parasites by these insecticides at any of the dose levels tested.

Greenhouse tests were conducted with the same insecticides, as well as the commercial crop oil Savol®. Individual excised cotton leaves were treated at one dose level and then aged in the greenhouse until they were brought into the laboratory, where they were infested with tobacco budworm eggs and then exposed to the parasites. When compared with the untreated control, parasitism was severely reduced in eggs exposed to parasites immediately after treatment with methyl parathion, methomyl, and permethrin. Somewhat lesser adverse effects were observed at the same time post-treatment in eggs sprayed with chlordimeform and thiodi-

carb. Thus, the greenhouse results closely paralleled those obtained in the laboratory.

Evaluations of the persistence of insecticidal activity against parasites in greenhouse conditions indicated that chlordimeform and thiodicarb were inactive at 1 day post-treatment, as was methomyl at 5 days. Methyl parathion and permethrin were the most persistent and they seemed to lose activity at about the same rate as they aged under greenhouse conditions. The severe reduction in parasitism by Savol was not unexpected, because previous laboratory tests had demonstrated that the parasites were adversely affected by crop oils (House et al. 1980). Although we did not anticipate the continued high level of inhibition of parasitism by aged residues of Savol, the results may help explain field observations of apparent adverse effects of crop oils on the performance of *Trichogramma.*

The results of studies of the direct dosage-mortality effects of different insecticides on *Trichogramma* adults exposed to treated surfaces in glass vials (Table 6) indicated that of the pesticides tested, parasites were least tolerant of methyl parathion and most tolerant of permethrin, a response comparable to that demonstrated for *Microplitis.*

Table 6. Toxicity of insecticides to Trichogramma pretiosum *adults*[1]

Insecticide	LC50s in μg/tube $\times$ 10^3
Methyl parathion	0.02
Methomyl	0.04
Dimethoate	0.16
Toxaphene	0.34
Chlordimeform	1.01
Phosmet	1.30
Permethrin	3.17

[1]From Bull and Coleman (1985).

Results of tests with *Trichogramma* show that broad-spectrum insecticides can severely inhibit the parasitism of treated host eggs by *Trichogramma.* However, these tests also indicated that the immature stages apparently are well protected from the effects of even the most toxic insecticides, once the parasite becomes established within the host egg. Although it is conceivable that carefully timed augmentative releases of *Trichogramma* could be used in conjunction with applications of selective insecticides to manage lepidopteran pests, such attempts must be preceded by thorough studies of the effects of specific chemicals on different life stages of the parasites, and of the persistence of biologically active residues of these chemicals on the target crop. In any case, it is likely that the integration of insecticide applications with *Trichogramma* releases would succeed only in a rigidly controlled management system.

In summary, both the laboratory and field experiments described in this paper have provided evidence in support of the hypothesis that some insecticides are safer than others for beneficial insects and therefore more likely to be compatible with the use of natural enemies for *Heliothis* management. The relatively safe insecticides are metabolized by hydrolysis or not at all, rather than by oxidation. By using such insecticides, differences in metabolic capabilities between pests and natural enemies may be exploited to obtain satisfactory selectivity. The foregoing information suggests ways to achieve even safer use of insecticides in the future, a usage compatible with the idea of conserving natural enemies of *Heliothis*.

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